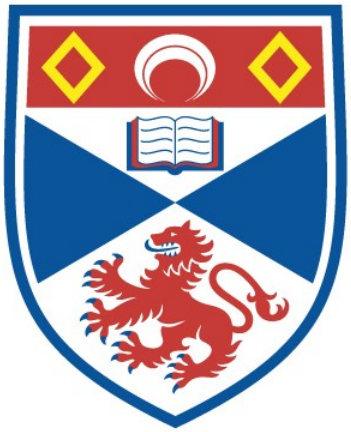
# A COGNITIVE APPROACH TO THE STUDY OF CULTURE IN WILD CHIMPANZEES (*PAN TROGLODYTES SCHWEINFURTHII*)

**Thibaud Gruber**

**A Thesis Submitted for the Degree of PhD**
**at the**
**University of St Andrews**



**2011**

# A COGNITIVE APPROACH TO THE STUDY OF CULTURE IN WILD CHIMPANZEES (*Pan troglodytes schweinfurthii*)

**Thibaud Gruber**

Thesis submitted for the degree of Doctor of Philosophy
School of Psychology
University of St Andrews
June 2011

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## Acknowledgements

It is always hard to find words to thank everyone after such a long journey. I hope I will not forget anyone, but having met so many during these last three years, I should apologise already if I do so.

First and foremost, my biggest thanks go to my supervisor, Klaus Zuberbühler. Klaus, you are basically the reason why I am in primatology today, by being the first to have allowed me to work with these wonderful animals. I will always fondly remember our first email exchanges. You have been an amazing supervisor and offered me the best environment I could work in.

I would like to thank the Leverhulme Trust for funding my research, and the Royal Zoological Society of Scotland for welcoming me in Edinburgh and Sonso to conduct my experiments and Fred Babweteera for providing excellent support and advice in the field.

Staying at St Andrews first, I would like to thank all the people who have been part of the Wolfson dungeon. Whether it was for discussing scientific stuff, heated debates, or simply social times, I had a great time down there. So thanks to Katie, Jessica, Verena, Cat, Gil, Felicity, Lisa, Rachel, Kate, Sally, Emily, Cris, Nuri, Marion and most especially to Zanna! Zanna, you are my academic great sister, and I will never thank you enough for all the things you've helped me with. From San Diego to Congo, we had some awesome times, and I owe much of my scientific approach to apes to your wise advice. Special thanks to the wonderful proof-reading team (Felicity, Verena, Rachel, Lisa, Sally, Emily, Maureen)! The remaining mistakes are all mine. At St Andrews, I would also like to thank Dick Byrne, who, as a second supervisor, brought a much needed critical view on my work, Andy Whiten, Juan-Carlos Gómez, Amanda Seed and Sue Healey for providing a great academic environment to discuss ideas and theories. Additionally, I thank everyone who participated to the BDG meetings. Finally, I would like to thank my great team of friends here at St Andrews who kept their friendship even when I was gone for so long: Gil, Laurel, Nicola, Alex, Eilis, Andy, Steve, Beryl, Darren, Valentina, Amy, Alice, John, Claire, Emily, Ed, Chris, Ben, Forbes, Alison.

In Uganda now, I would like to thank everyone who helped me to conduct my work in Budongo and Kibale forest. Permission to conduct research was given by Uganda Wildlife Authority (UWA), Ugandan National Council for Science and Technology (UNCST) and National Forestry Authority (NFA) and I am very thankful to everyone who assisted me in obtaining the permits and extensions in sometimes amazingly short times. I am also very thankful to Richard Wrangham and Martin Muller for accepting to let me conduct my experiments in Kanyawara.

I could not start anything about Budongo without thanking first Roman Wittig and Cathy Crockford for everything. You guys are just some of the most amazing people I have ever met and your support and help throughout my stay was incredible. I would also like to thank Vernon Reynolds for starting

this great project and his precious discussions and advice. At Sonso, I would like to thank all the long-term researchers I have overlapped with: Anne, Tanja, and Caroline, as well as Katie Slocombe. We've been through so many great times, but also had to cope with really bad times as well, and I will remember fondly that we have always remained a great team together.

At Sonso, I have so many people to thank but the most important person is Steven. Steven, you were a wonderful assistant and the success of my experiments owes much to your expertise of the chimps, your carpentry skills, and your talents in negotiating good deals in the village! I also thank fondly all the assistants who were of great help and great fun in the forest: Geresomu, Monday, Jackson, Jacob and Sam. Sadly, James passed away a few months after I left and I fondly remember him, as well as Richard, who was a true friend. At camp, nothing would go right without the expertise of Zephyr, in addition to his qualifications as my personal 'mango fly doctor'. I also thank Mary and Sarah for the cooking and house-keeping work. I am very grateful to Chris, Susan, Maisie-Rose and Connie to have accepted the challenge of implementing my experiments in sometimes hard conditions. Thank you very much, and I hope your training in Uganda will help you for future research. Additionally, I would like to thank Amos Wekesa, Baylon Iga and Doreen Kafureka at Great Lake Safaris and for assistance in the field, I would like to thank James Kyomuhendo and Emily Otali at Kanyawara, Nyoli and Butele Lino at Kaniyo Pabidi and Vincent Odama and Chombe Deo at Busingiro. In Kasokwa, finally, I would like to thank Maureen McCarthy and Brittany Fallon.

Back in Europe, there are some people who I could not forget to mention, even if they may not be aware of their contribution. So thank you to Christine Saux, for being such a great biology teacher; to Philippe Gillet, for believing in me; and to Franck Ramus, who was always supportive of my projects.

I will not forget to thank my friends and family at home, who have all been very supportive of my work from the early beginning. My mum likes to say that some of the first words I said were that I wanted to become a 'doctor for animals'. Well, finally, I may indeed end up as a doctor, with a specific interest in animals. Not so far... Sylviane, Michel, and Guillaume (sans oublier Marion, qui est déjà de la famille!), merci mille fois de votre amour et d'avoir toujours supporté mes étranges passions! Merci de m'avoir fait voyager très tôt de par le monde pour découvrir d'autres cultures, et merci d'avoir toujours tenté de combler ma curiosité insatiable !

Finally, this thesis would not have existed without the amazing apes I have been working with. So, thank you to Manono, Tatango, Mimi, Semendwa, Kikwit, Nambi, Nora, Night, Musa, Squibs, Hawa, Nick, Tinka, Sabrina, Kakama, Quinto, Wilma, Tuber and all their fellows for allowing me to live part of their lives and attempt to understand them. Many of them suffered because of humans, and they are only the tip of the iceberg I was in contact with. As such, this thesis is dedicated to all the apes who are still inhabiting their native wild forests, with the hope that getting to know them better will allow us to prevent them from becoming extinct.

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# Abstract

The question of animal culture has been of interest for decades. Chimpanzees (*Pan troglodytes*) have played a key role in the debate of whether or not it is appropriate to use the term 'culture' to describe animal behaviour and they continue to be one of the prime species for the study of the origins of human culture. Data suggesting that chimpanzees can be considered a cultural species continue to accumulate, but this has only enhanced the debate between proponents and opponents of animal culture. Opponents do not deny that behavioural diversity exists between different populations of the same species, but they maintain that such phenomena have little to do with human cultures and may be the result of genetic and environmental influences. In their view, human cultures are centred on socially shared sets of ideas, not behavioural traditions. In this thesis, my goal is to tackle this problem and to investigate whether a cognitive dimension can be found in some behavioural patterns of chimpanzees that have been put forward as examples of animal culture. To this end, I examine the different factors that could account for the development of tool use in animals (genetics, ecology, social). My first empirical contribution is a study of the tool use behaviour of the chimpanzees' closest relative, the bonobos, which are known to be limited tool-users in the wild. I show that captive bonobos are as flexible tool-users as chimpanzees, suggesting that genetic factors are unlikely to account for differences in tool use behaviour in the *Pan* clade. Second, through the use of field experiments, I show that wild chimpanzees from different Ugandan communities respond to the same apparatus and task in strikingly different ways. I interpret this finding as an outcome of differences in cultural knowledge, mainly because the affordances of their immediate environment do not determine their tool use behaviour. Finally, through a broad ecological and tool use survey of different chimpanzee communities in Uganda, I show that current ecological differences are poor predictors of tool use. I conclude that, if ecology plays a role in the development of tool use, then its influence is that of a selective force. Finally, when reviewing the outcome of this research I will argue that there is a profound cognitive dimension to tool use in wild chimpanzees, suggesting that behaviourally based definitions of animal culture may miss a key feature of the phenomenon, at least in chimpanzees. Chimpanzees are not only a cultural species, they also have a cultural mind.

# Chapter one: Introduction – Tool use & Culture in animals: The never ending debate

"Now we must redefine tool, redefine Man, or accept chimpanzees as humans."

Louis Leakey (1960)

"Labelling ape behavior as “culture” simply means that you have to find a different word for what humans do." Jonathan Marks (2002)

Parts of this introduction have been published in the following review paper:

**Gruber, T.**, Reynolds, V. & Zuberbühler, K. (2010) The knowns and unknowns of chimpanzee culture. Communicative and Integrative Biology, 3(3): 221–223.

and are in preparation for submission in the following review paper:

**Gruber, T.** & Zuberbühler, K. The Jourdain hypothesis: Chimpanzees have culture, but they don’t know that they do. *In prep.*

## Summary

In this first chapter, I introduce the different notions which will be explored in this thesis. In the first part of the introduction, I review animal tool use from both a biological and a cognitive point of view. I also review data from the primate taxa, recognised widely as the most sophisticated tool-users of all, and I introduce the two species of interest in this thesis: the common chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*), particularly focusing on their respective socio-ecology and their differences in tool use. The second part of the introduction deals with culture in animals and humans. I explain firstly how tool use is related to culture, and why, while tool use appears uncontroversial in animals, culture is. A particular focus will be on the social learning mechanisms, which play a key role in the development of culture. I then present the different approaches which have been designed to show culture in animals, the criticisms that they have fostered, and more generally the different schools of thought in order to illustrate the ongoing debate between animal culture proponents and sceptics. At this point, I introduce recent paradigms used to study human cultures, to show how different they have become from those used by animal researchers. I also present field experiments and show how they can be used to study culture in animals. Finally, I conclude that the animal culture debate arises mainly from different definitions and that this debate is more of a Red Queen's race which may not evolve much further. This situation urges the need to change paradigm if we wish to end up with strong conclusions.

Animal tool use has always been fascinating for humans, who have long believed to be the only tool-makers in the animal kingdom (Oakley 1959). Animals, notably chimpanzees who became famous thanks to Wolfgang Köhler's experiments in Tenerife (Köhler 1921), had long shown their abilities to use tools in captivity. However, the first observations of tool-making in wild chimpanzees by Jane Goodall during the first stages of her stay at Gombe in 1960 was a major scientific advance (Goodall 1964). Louis Leakey's telegram reacting to the discovery highlighted its importance: another animal species on earth other than humans was able to make tools to attain a certain goal, in this case, fishing for termites.

Chimpanzees have since become a prime model to study tool use and to understand the evolution of our own tool-using abilities (McGrew 1992). In this respect, tool use is interesting from a number of perspectives, as this ability relies in humans on a number of cognitive traits such as developed physical cognition, a sense of causality or a sense of planning, to cite a few. Thus, understanding if such traits are also used during animal tool use informs us on how similar tool use is in humans and non-human animals (for the rest of the thesis, abbreviated as 'animals'), on what has possibly evolved in our common ancestors, but also on what has likely only evolved in our lineage after we split with the *Pan* genus.

Animal tool use has also been of interest during the last forty years with respect to its connection to culture. McGrew pointed out that most of animal cultures is material (McGrew 1992), and tool use has indeed the lion's share in the list of chimpanzee presumed cultural variants (Whiten et al. 1999, 2001). The scientific debate on tool use aims to estimate animal tool use extent and characterise how much of it animals actually understand. In contrast, the claim that chimpanzees and then other species had culture (e.g.: whales and dolphins, Rendell and Whitehead 2001; orangutan, van Schaik et al. 2003) triggered many debates which sometimes tended to oppose philosophical stances rather than clear scientific positions. These stay unresolved as of today, as can be inferred from Jonathan Marks' quote.

In this thesis, I will mainly address the question of culture in wild chimpanzees. However, to understand the ins and outs of the debate and to tackle some of the issues raised, I will first present animal tool use in a broader perspective within a large number of taxa; then I will describe the cognitive questions that are at stake. This will be done in the first part of this introduction, which will also introduce the two species in the *Pan* genus, the chimpanzee and the bonobo. In the second part of the introduction, I will then present more specifically the questions that are of concern in the cultural debate.

# A. Animal tool use: A wide range of data and questions

## 1. Animal tool use

### A wide range of tool-using species and of approaches to analyse tool use

Tool use has been observed in numerous species and taxa, such as insects, birds, marine mammals or primates (Eibl-Eibesfeldt 1961; Beck 1980; Whiten et al. 1999; Rendell and Whitehead 2001; Lefebvre et al. 2002; van Schaik et al. 2003; Krützen et al. 2005; Bentley-Condit and Smith 2010). A widely accepted definition of tool use in animals is the use of an "unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (Beck 1980, p. 10). However, it is unclear if other borderline cases, such as: the use of water to catch a prey or a reward (fish: Lüling 1963; orangutan: Mendes et al. 2007); the use of a hard surface to crack open a shell (birds: Lefebvre et al. 2002); or nest building (Hansell and Ruxton 2008) should be considered tool use (Seed and Byrne 2010).

Interestingly, the use of water as a tool illustrates a second problem when comparing species. While laypeople and scientists alike would not say that archerfish understand that they are using water 'as a tool', they would probably be more likely to say orangutans do. Similarly, the case of the ant-lion larva throwing sand out of its nest (which in effect causes a prey to fall into its trap) would not be analysed the same way as the cases of baboons or gorillas throwing rocks at predators (Seed and Byrne 2010). As a matter of fact, if we were to witness humans performing the same behaviours, we would not even consider that they do not think about what they are doing. In other words, we attribute to humans the ability to mentally represent what they are doing. We are also likely to attribute this ability to represent to chimpanzees, orangutans or baboons to a certain extent, although we may not go as far as attributing to them the same ability we attribute to humans. Finally, most of us would not attribute such an ability to fish, feeling that an explanation based on 'instinct'or on an innate programme would explain this behaviour. Therefore, there seems to be different levels of

tool-using, with species able to represent wholly or partly the concepts attached to tool use, and, on the contrary, species that are not thought to be able to do so.

Similarly, some commentators have pointed out that some tool-using behaviours may be more 'intelligent' than others. Parker and Gibson (1977) have highlighted that primate tool use is especially flexible and therefore, denotes a "true tool use", compared to an inflexible tool use that they attribute to other species. However, this view is not shared by everyone. Even though his own list has shown that most tool use in the animal kingdom is overspecialised (many species having only one or a small number of tool-using techniques), Beck contests the fact that predatory shell dropping in some birds would be "unintelligent", based on Parker and Gibson's criterion (Beck 1980, p. 210). These examples illustrate that the debate on tool use is broad, and that all of its aspects, from the genetic bases to the mental representations of tool use, should be studied.

**Genetic components of tool use**

The fact that presumably 'cognitively simple' animals, such as ants or archerfish, possess certain tool-using behaviours suggests either that tool use can have a strong innate origin or that our perception of these species' cognition is mistaken. Fish cognition, for instance, has been shown to be very developed (Brown et al. 2011). Additionally, many of our own tool-using behaviours depend on our genetic background. Simply observing our morphology, notably our opposable thumb, a critical component of our prehensile hand, shows that it is very well adapted for using tools. However, species like bottlenose dolphins lack hands and are still able to use tools such as sponges that are carried on the rostrum (Mann and Sargeant 2003). More generally, as our behaviour is the result of an interaction between genes and environment, our abilities for representing objects as tools or to understand their affordances depend on genetics in the first place. The debate, though, centers more on which aspects of tool use behaviour are not genetic, rather than which are. In humans, most of the tools we are using now are the result of thousands of years of cumulative cultural evolution rather than biological evolution (Tomasello 1999). The amazing accumulation we observe in humans depended on a critically flexible mind, unrivalled in the animal kingdom, which allowed us to overcome much of our biological evolution and to complete it with a cultural evolution (Whiten 2005). If human tool use was only the result of innate abilities, it could not have possibly evolved at the speed it has, notably since the industrial revolution started.

As tool use was long thought to be exclusively human, it was also natural to think that only more closely related species to us would be able to manufacture tools. The ability to use tools is one thing, but the ability to manufacture them is another and requires additional abilities. For instance, it implies to be able to produce an object as a means to reach a goal and involves additional planning. Thus, the discovery that New-Caledonian crows were capable of manufacturing tools (Hunt 1996) was of prime importance, given the evolutionary gap between crows and humans. This suggested that convergent evolution could bring a species whose brain is organised very differently from ours to also develop tool manufacture (Seed et al. 2009b; Fig. 1.1). But, is bird tool-making really similar to primate tool-making? Subsequent experiments with captive-born and human-raised crows showed that naïve individuals, even when they had never witnessed any other individual from their own or another species manufacturing tools, could also readily start doing so, with no difference between individuals which had not been socially exposed to tool use and ones which had (Kenward et al. 2005), suggesting a strong genetic component in this behaviour. Additionally, successful recent tool-using experiments with rooks, which are of the same family as the crows but are non-tool users in the wild (Seed et al. 2006; Bird and Emery 2009a, b) suggest that the genetic components in tool-using abilities in crows have to be taken into account.

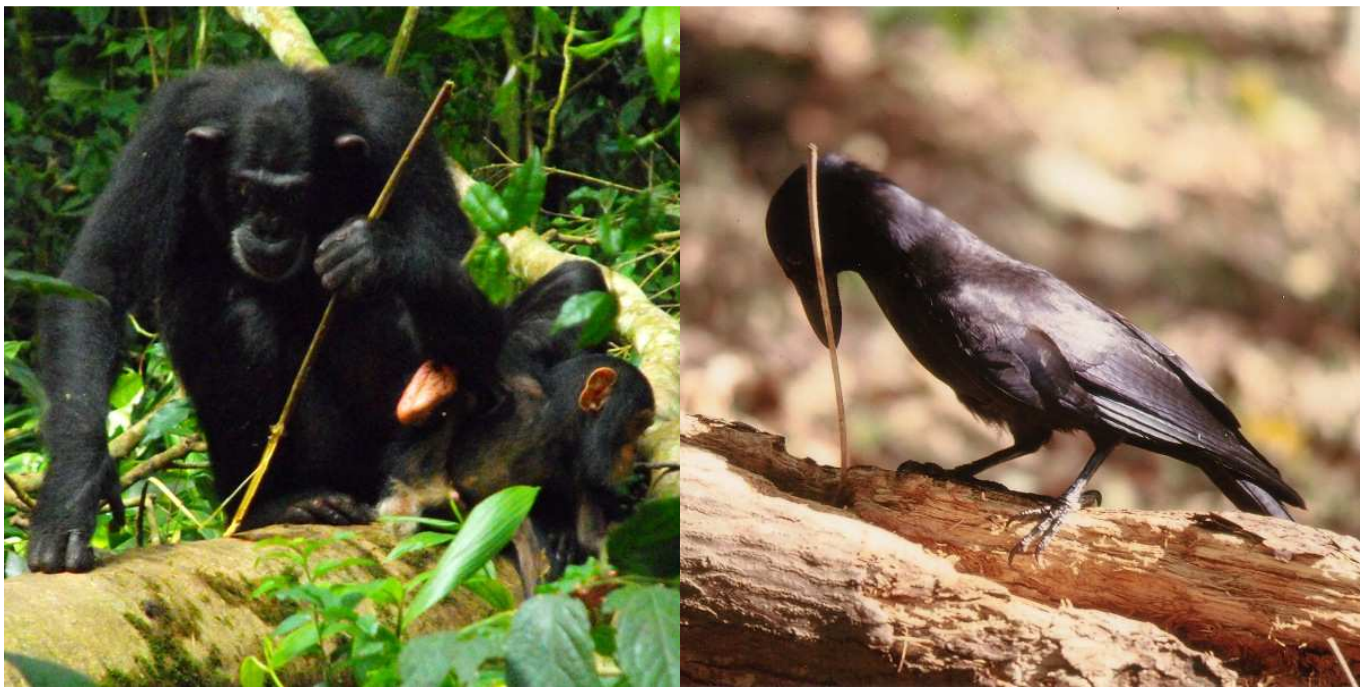

**Figure 1.1.** Avian and primate tool use compared (chimpanzee picture courtesy of Paco Bertolani, New-Caledonian Crow picture courtesy of Gavin Hunt).

**Physical cognition**

While the studies with crows and rooks show that there is an innate component in tool-using abilities in these species, they also show that the cognitive abilities at work during the tool-using tasks are far from limited (Seed et al. 2006; Bird and Emery 2009a, b). These studies have indeed shown that rooks are able to use a diversity of tools for the same task, to modify a tool to adapt it to another task (e.g., a wire turned into a hook), or to use tools in sequence to attain a certain goal. This flexibility shows that a strong genetic basis does not preclude developed cognition in tool use.

Similarly, following Parker and Gibson's assertion that primate tool use is more intelligent than other species tool use, studies in primates have long attempted to test if such was the case. The results over the years have been mixed. Primate understanding of tool use has been extensively described by Visalberghi and colleagues notably through the use of the trap-tube task, which involves recovering a reward in a tube while avoiding a trap (e.g. Limongelli et al. 1995). Their conclusions were that contrary to capuchin monkeys, apes and chimpanzees in particular, showed some understanding of the tasks that were proposed (Visalberghi et al. 1995). Tomasello and Call (1997) pointed out that the tasks proposed by Visalberghi and colleagues were "fairly difficult conceptually" (p. 95) and primates, monkeys included, have been more successful in simpler tasks that involve spatial causal cognition such as the support task, which consists in choosing between two cloths to recover an out-of-reach reward, one having the reward on it but the other having the reward off it (Mathieu et al. 1980; Natale 1989; Spinozzi and Potì 1989, 1993). Recently, it was also shown that wild capuchin monkeys were able to assess the suitability of experimentally provided stone tools to crack nuts, showing that they represented different physical properties of these tools (e.g. weight against appearance) to select the proper tool (Visalberghi et al. 2009).

However, in most studies, only few individuals succeed in the proposed tasks and they rarely show unequivocal proof that they understand the tasks at stake (Povinelli 2000). For instance, in the trap-tube task, chimpanzees continued to avoid the trap even when the tube had been turned so that it faced up (thus becoming irrelevant to the task), suggesting limited physical cognition (Povinelli 2000). These results led some researchers to suggest that chimpanzees do not understand much about the physical properties of objects and to favour a model based on perceived features rather than on an abstract knowledge of the properties of the tools (Povinelli 2000). Nonetheless, the fact that human participants behaved similarly when

confronted to this task clearly questions its suitability to draw such conclusion (Silva et al. 2005). Recently, Seed and colleagues (2009a) showed that chimpanzees solved a modified trap-tube task, which did not include the use of a tool. One individual could transfer her knowledge to another task, showing that she had acquired some information about the functional properties of the objects she was dealing with rather than superficial perceptual features only.

**Causality, planning and foresight**

Using tools 'intelligently' does not only require representing the functional properties of a tool, it also requires being able to understand the effects of its action. As mentioned above, it is unlikely that ant-lion larvae represent the causal relationship between throwing sand and catching a prey as a reward. This behaviour would thus likely be described as innate, although gene-environment interactions must be taken into account. However, when dealing with humans, a number of cognitive abilities appear to be linked to tool use. We know why we use a certain tool, its purpose, its order of use in a particular sequence, and we know that the tool and our particular usage of it are part of a causal chain of events that leads ultimately to our final goal. It has been difficult to define causality (Hume 1739/2000; Collingwood 1972; Tomasello and Call 1997) but the concept of representation is central. Causality requires understanding that the contiguity of two events is linked and that one of them provokes the other one. This ability is central when trying to achieve a goal. Animal data give a different picture, depending on the study species. When chimpanzees or capuchins crack nuts, we assume that they do so with the intended goal of obtaining the kernel inside the hard shell. However, naïve New-Caledonian crows engage spontaneously with a stick and manage to use it 'correctly' without being prompted to do so and without any apparent goal in mind, appearing less likely to have an understanding of what they are doing (Kenward et al. 2005). However, the insightful use of tools by naïve rooks makes the picture even more complex by questioning whether a strong genetic component in tool-using abilities would be incompatible with an understanding of the tasks at stake (Bird and Emery 2009a).

Both insight and foresight are integral to human tool use. The distinction between these two types of reasoning was proposed by Köhler and distinguishes respectively "quickly recognising when the right solution has been stumbled upon in the course of exploration, leading to a sudden disappearance of further trial-and-error" and "sizing up a problem in

advance through physical reasoning and bringing a new solution to it fully formed" (Seed and Byrne 2010, R1035). Whether these two types of reasoning are also part of animal tool use is still debated, as what appears to be insight could be explained with less anthropomorphic mechanisms relying on prior knowledge (Shettleworth 2009; von Bayern et al. 2009).

Finally, planning is also of prime importance in human tool use. Chimpanzees are known to carry suitable hammers to nut-cracking sites (Boesch and Boesch 1984) and apes, in general, are able to save tools for future tasks, sometimes for a long period of time (Mulcahy and Call 2006a; Osvath and Osvath 2008). Similar observations have been made in corvids and capuchins (Visalberghi et al. 2009; Seed and Byrne 2010). Although caution must be taken for the interpretation of these behaviours as they might only be the result of a learnt habit and not include a representation of future tasks as in the human case (Raby and Clayton 2009; Shettleworth 2010), some observations in chimpanzees argue in favour of a certain level of representation. At Goualougo, some tool use requires the consecutive use of two types of sticks to fish for underground termites (Sanz and Morgan 2007), and at Bossou, meta-tool use, defined as "the use of a tool to produce or enhance the effectiveness of another tool" (Matsuzawa 1991; Sousa and Matsuzawa 2006 p. 412), has been observed. Meta-tool use has recently been described in New-Caledonian crows, and their capability to abandon it when it was not necessary anymore also supports an intelligent understanding of tool use in this species (Taylor et al. 2007).

In any case, the debate on causal cognition is not resolved yet and the true impact of causal cognition on tool-using abilities still has to be determined (Tomasello and Call 1997; Shettleworth 2009; von Bayern et al. 2009; Seed and Byrne 2010).

## 2. Primate tool use

Of all animal species, primate species are the unrivalled tool-users (Bentley-Condit and Smith 2010). For instance, Lefebvre and colleagues' extensive study on birds found a total of 120 tool-related behaviours over 104 species, classifying only 39 of these as true tool use (Lefebvre et al. 2002). In comparison, Reader and Laland (2002) reported 607 cases in their analysis of approximately 1,000 journal articles covering 116 primate species. Here, I will

present the most famous examples of primate tool-users, which frequently use tools in their natural habitat: tufted capuchins, macaques, orangutans and common chimpanzees.

**Monkeys**

Compared to chimpanzees, capuchin tool use in the wild was reported only recently (Ottoni and Mannu 2001; Fragaszy et al. 2004; Ottoni and Izar 2008), although it was known for a long time that they were keen tool-users in captivity (Fragaszy and Visalberghi 1987; Visalberghi 1987, 1990). In the wild, capuchin tool use is nearly exclusively stone-aided nut-cracking. However, some groups of the *Cebus libidinosus* species have also been observed using stones to dig the soil while foraging for roots, as well as for breaking open wood to consume the insects and larvae it contains (Moura and Lee 2005; Ottoni and Izar 2008). Interestingly, out of the four species found in Brazil, only *C. libidinosus* and *C. xanthostemos* are thought to use tools, while evidence for tool use in *C. nigritus* and *C. apella* is missing. However, Ottoni and Izar (2008) doubt that genetic differences can account for this observed difference as interbreeding occurs in a number of semi-free groups under study, which do not show behavioural differences in terms of tool use. Additionally, many captive studies were conducted with *C. apella* individuals whose species is thus 'genetically able' to use tools. Recently, combined use of sticks and tools and apparent meta-tool use has been found in two populations (Mannu and Ottoni 2009). However, no tool use has been documented for a social purpose (e.g. communication), which contrasts with results reported in ape species. Tool use has also been described in several species of macaques, which have been observed using sticks for dipping (Babitz 2000) or using pounding hammers (Gumert et al. 2009).

**Orangutan**

Apart from chimpanzees, orangutans are the only apes known to use tools on a regular basis in the wild (van Schaik et al. 1996; van Schaik and Knott 2001; van Schaik et al. 2006; Russon et al. 2009; van Schaik 2009; van Schaik et al. 2009a). Tool use is observed during food acquisition (e.g. van Schaik and Knott 2001) but also during self-cleaning and in social contexts. A famous example is the enhancement of the kiss-squeak, a vocalisation that orangutans produce when they feel threatened, by the use of leaves. This behaviour may even have acquired a deceptive function (Hardus et al. 2009; Fig. 1.2). Other interesting cases

include tools used for sexual stimulation, or the use of leave-gloves to touch spiny objects or break into ant nests (van Schaik et al. 2009a).

Recently, the two former subspecies of the genus *Pongo* have been described as two different species, depending on which island they are found: the Sumatran orangutan (*Pongo abelii*) and the Bornean orangutan (*Pongo pygmaeus*), which is further divided in three subspecies. However, the point is still contentious, because even if these two species have clear morphological and genetic differences, they can nonetheless interbreed in captivity (Goossens et al. 2009). They also differ in some of their tool-using habits. For instance, some behaviours (e.g., scratch with stick, which is self-explanatory) have only been observed in Bornean populations, and not in the Sumatran ones. However, a careful examination of behavioural variations between the two species, and notably the high intraspecific variation observed in Bornean populations (some populations do not show the said behaviour while others do at a customary frequency) rule out that genetic differences would explain these observed differences (van Schaik 2009).

**Figure 1.2.** Orangutan performing leaf-enhanced kiss-squeak (courtesy of Madeleine Hardus).

**Chimpanzee**

Chimpanzees (*Pan troglodytes*) are the most famous animal tool-users. Known for a long time to be very flexible in their uses of tools, they were the species Wolfgang Köhler observed and from which he defined the notion of insight (Köhler 1925). The first reports of tool use in wild chimpanzees date from the missionary work of Thomas Savage (Savage and Wyman 1844), but the first scientific observations were provided by Jane Goodall (Goodall 1964). Since then, observations have been continuous in many sites, including Gombe for the last fifty years (Lonsdorf 2010), and a number of communities could be studied for more than twenty years with no interruption (Whiten et al. 1999). Chimpanzee tool use has been found to be extremely diverse and is found both during food acquisition processes and for social purposes (McGrew 1992, 2004). Additionally, the complexity of tool use observed in this species is unrivalled among other animals, with the notable use of meta-tools (Matsuzawa 1991) or complex sequential use of tools (Sanz and Morgan 2007). The most complex sequence of tools has been described in a Gabonese population where no less than five successive tools with different functions are being used to fish for honey (Boesch et al. 2009).

An interesting point is that different communities have different tool use repertoires. For instance, Western African chimpanzees were thought for a long time to be the only nut-crackers (Boesch and Boesch 1990; Boesch et al. 1994) as no Eastern chimpanzee population had been observed cracking nuts. However, recent observations of nut-cracking in Cameroon showed that this behaviour was more widespread in the wild than expected (Morgan and Abwe 2006; Wrangham 2006). In other sites where nuts are present and for which long-term observational data are available (allowing one to dismiss any claim that the reported absence is due to an observation bias), nonetheless, some communities appear to ignore them (McGrew et al. 1997).

Additionally, one community of chimpanzees may use the same exact behaviour as another community in another part of Africa for a radically different purpose, showing the extent of chimpanzee tool use flexibility. For instance, leaf-clipping, which consists in tearing apart leaves in order to produce a recognizable noise, is used in Budongo or Mahale to attract a female's attention during courtship, while it is used in Taï and Bossou to signal frustration (Whiten et al. 2001).

**Different populations, different levels of tool-use**

A last point to mention is that there is no such thing as a representative population or community of capuchins, orangutans or chimpanzees. Although chimpanzees are famous for their tool-using abilities, not all populations are great tool-users. For instance, while most populations' tool catalogues are of about twenty different behaviours, long-term habituated Ugandan populations (Budongo, Ngogo and Kanyawara) have only been found with about ten of such behaviours (Whiten et al. 1999; Watts 2008; McGrew 2010). Among these, the Budongo chimpanzees are famous for having never been observed using sticks in over twenty years of continuous observation (Reynolds 2005). Ecological explanations can hardly explain such differences as sometimes, populations inside the same continuous forests are observed with different tool-using patterns, such as the Mahale K and M groups. The former were never observed to fish for termites, while the latter do it on a customary basis.

Similarly, variations are found between communities of orangutans that share the same genetic background, such as the orangutans of Suaq Balimbing and Ketambe, both found in Sumatra. The Suaq community is using tools in many more ways than the Ketambe one, notably while foraging for honey. A number of studies have attempted to explore the reasons for this difference (van Schaik 2003; Fox et al. 2004; van Schaik 2009). While a genetic explanation is unlikely, ecology may have a role in this variation because of the differences in substrate availability in the two sites. However, this ecological factor cannot explain the complete absence of the behaviour in Ketambe (van Schaik 2003; Fox et al. 2004).

The capuchin data also shows important variations. Apart from the genetic differences already mentioned, some populations in Serra da Capivara appear very different in their tool-using techniques in comparison to the other tool-using capuchin populations (Mannu and Ottoni 2009). Although the authors acknowledge that a number of ecological differences could account for some of the observed differences, they think that a social explanation is more appropriate to explain the overall variation (Ottoni and Izar 2008).

Finally, it is noteworthy to mention that although chimpanzees are the most complex animal tool-users, their sister species, the bonobo (*Pan paniscus*) are much less renowned for their tool-using abilities, which are much more limited (see below, Hohmann and Fruth 2003a). Bonobos and chimpanzees will be the two species of study in this thesis. Thus, I will now describe their socioecology, behaviour and characteristics in a comparative way, so as to highlight their differences and similarities.

## 3. Chimpanzee and bonobo: The sister species

### Speciation, genetics and morphology

While the chimpanzee was already studied in the late XVIII $^{th}$ century, the bonobo was only recognised as a species in 1929 following Schwarz's careful morphological analysis of a skull in the Tervuren museum, Belgium, and subsequent studies by Coolidge (Schwarz 1929; Coolidge 1933). Since this time, genetic data have documented the separation between the two species and their estimated split is set around 0.9 million years ago (Won and Hey 2005). Based on both early morphological (Schwarz 1934; Hill 1969) and more recent genetic analyses (Morin et al. 1994; Gagneux et al. 1999; Kaessmann et al. 1999), chimpanzees have been separated into three subspecies: *Pan troglodytes verus* (Western African chimpanzee), *Pan troglodytes troglodytes* (Central African chimpanzee) and *Pan troglodytes schweinfurthii* (Eastern African chimpanzee). Another subspecies, following the discovery and study of populations between the lower Niger River and Cameroon has been proposed as *Pan troglodytes vellerosus* (Gonder et al. 1997; Gonder et al. 1999) or *Pan troglodytes ellioti* (Oates et al. 2009) but the existence of this potential new subspecies is still under debate (Becquet et al. 2007). Additionally, all studies find that *P. t. verus* is clearly different from *P. t. troglodytes* and *P. t. schweinfurthii* as a group, suggesting that *P. t. verus* could be considered as a separate species in its own right (Morin et al. 1994; Gagneux et al. 1999). Finally, altogether, the common ancestor of chimpanzees and bonobos is assumed to have diverged from the human lineage around 5 to 7 million years ago (Gagneux et al. 1999; Stone et al. 2010) although some studies place the split even later (Hobolth et al. 2007).

The variety of subspecies in chimpanzees, in comparison to the absence of subspecies in bonobos, illustrates a major difference between the two species: the chimpanzee range in Africa is much wider than the bonobo range. While chimpanzees are found from Western to Eastern Africa, bonobos are confined to the Cuvette Centrale region of northern Democratic Republic of Congo, delimited by four rivers: the Congo, Kasai, Lualuba and Sankuru Rivers (Toham et al. 2006; Clay 2010; see Fig. 1.3).

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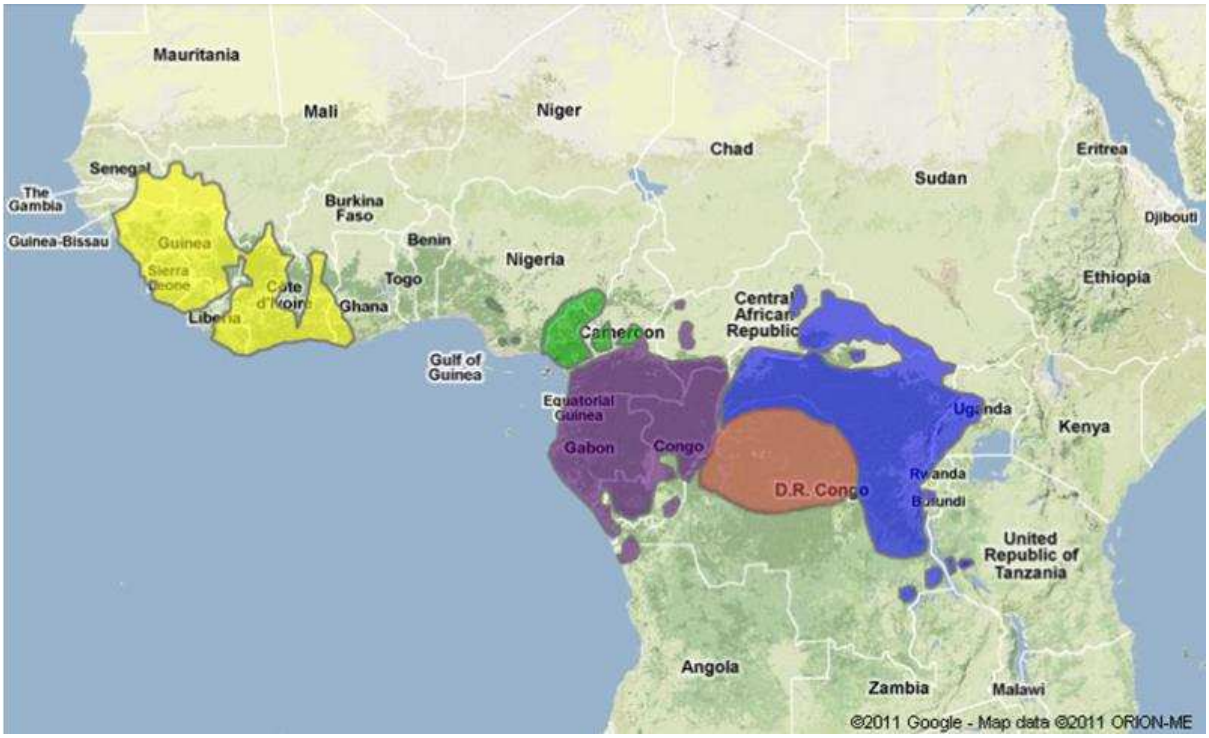


**Figure 1.3.** Map showing the repartition of chimpanzee subspecies (yellow: Western, green: Nigerian-Cameroon, purple: Central, blue: Eastern) and bonobos (red) in Africa (© 2011 WWF (panda.org) and Google –Map data. Some rights reserved).

Morphologically, chimpanzees and bonobos may look similar to laypeople and non-habituated eyes. Although frequently referred to as pygmy chimpanzees, bonobos are not smaller than common chimpanzees. Their bodies however are slender, which can create this impression. Bonobo faces are generally darker than those of chimpanzees. Additionally, bonobos are born with a characteristic black face, in contrast to chimpanzees whose face colour is pale during infancy before darkening (de Waal and Lanting 1997). In both chimpanzees and bonobos, sexual dimorphism is low, males averaging about 43 kg and females about 37 (Parish 1994; de Waal and Lanting 1997). Another distinct difference between chimpanzees and bonobos, on which Schwarz founded his discovery, is the shape of their cranium (Lieberman et al. 2007). These anatomical differences have led researchers to suggest that bonobos have been subjected to an evolutionary pressure towards neoteny (which means that they retain juvenile characteristics in their adulthood). This was first proposed because of their morphology (Shea 1983; Wrangham and Pilbeam 2001) but this finding has now been complemented by behavioural observations (Wobber et al. 2010).

**Feeding ecology**

In Wamba, Hashimoto and colleagues (Hashimoto et al. 1998) distinguished three types of forest (dry forest, swamp forest and disturbed forest) and found that bonobos preferred to stay in the dry forest, although they visited the two other forests every day as they provide important additional food on a yearly basis. The three types of vegetations offer indeed different kinds of food. The dry forest is mainly composed of primary forest, and of some old secondary forest. It offers a number of fruit trees consumed by bonobos, notably their favourite species (Kano and Mulawa 1984). On the contrary, swamps and secondary forests contain abundant herbaceous food which is also used during fruit seasons transitions in Wamba (Kano 1992; Hashimoto et al. 1998). However, White (1998) did not find a significant inverted correlation between the use of figs, other fruits and terrestrial herbaceous vegetation ('THV' for the rest of the thesis) and found no significant times of food scarcity altogether in comparison to chimpanzees sites. In addition to these food sources, bonobos also feed on honey, mushrooms and meat (Badrian and Malenky 1984; Hohmann and Fruth 1993; Bermejo et al. 1995; Surbeck and Hohmann 2008; Surbeck et al. 2009). Finally, although most studies have been conducted in forested areas, bonobos have also been found in more savanna type areas (Myers-Thompson 2002). These observations thus suggest that their supposed limited range may be due to the limited number of field sites rather than to an actual limitation of their ecological flexibility (Clay 2010).

Similarly, chimpanzees are primarily thought to live in the tropical forest, but they can be found in very different habitats, ranging from rain forests to grassland and woodland up to savanna type areas (McGrew et al. 1981; Goodall 1986; Boesch and Boesch-Achermann 2000; Reynolds 2005). Chimpanzees living as close as 12 km apart can also live in very different environments and thus have different diets (Potts et al. 2009; Potts et al. in press). Dietary preference can thus vary strongly between neighbouring communities: in Kibale National Park, Uganda, the Kanyawara chimpanzees rely heavily on THV as part of their diet (Wrangham et al. 1996), while Ngogo chimpanzees consume THV very rarely although it is present in their environment (Potts et al. in press). Although fruits are the bulk of their diet, chimpanzees also eat meat and have been observed hunting for monkeys and small mammals (Boesch 1994; Stanford et al. 1994; Watts and Mitani 2002; Pruetz and Bertolani 2007). I will provide a more developed discussion of chimpanzee ecology in chapter 6.

**Social and dominance systems**

Chimpanzee and bonobo societies are both philopatric societies where females emigrate at adolescence while males remain in their natal group (Goodall 1986; Kano 1992). However, their social system is very different.

The chimpanzee society is usually described as male-centred, with males heavily involved in building coalitions and alliances to raise in power (de Waal 1982; Goodall 1986; Wrangham 1986; Wrangham and Peterson 1996; Mitani et al. 2000). On the contrary, females have often been considered less involved in the group 'politics' and to occupy defined ranges within the community range where they remain most of their time (Wrangham and Smuts 1980). However female ranges appear to be correlated with the richness of the food provided and the rank of the females who occupy them, showing that there is also a strong reproductive competition between females (Pusey et al. 1997; Murray et al. 2006). Recent data have begun to question the apparent female passivity in the group social life (Muller 2007). Females, as well as males, engage in infanticide (Townsend et al. 2007) and recent studies highlight how females get involved in social life and form strong bonds between each other (Langergraber et al. 2009; Lehmann and Boesch 2009). Finally, the chimpanzee society is very hierarchical and subordinate individuals show their submission to dominants through the use of a specific vocalisation: the pant-grunt (Noë et al. 1980), although the control of the production of this vocalisation is audience-dependent (Laporte and Zuberbühler 2010).

In contrast, the bonobo society has usually been seen as a peaceful, egalitarian, female-dominated society (Parish 1994; de Waal and Lanting 1997). Although this view has been contested (Stanford 1998), females maintain strong bonds together which allows them to dominate over males. Males are less likely to form bonds with each other; however they form strong bonds with certain females, notably their mother (White 1989; Furuichi and Ihobe 1994; Furuichi 1997; Hohmann and Fruth 2003b; Surbeck et al. 2011). In general, males do not seem to be concerned with dominance ranks, although a hierarchy still exists between them (Furuichi 1997). Although present in bonobos, pant-grunts are not a reliable indicator of dominance and methods based on the analysis of displacement must be used instead to assess the group hierarchy (Stevens et al. 2007; Clay 2010). Finally, bonobos are notorious for their frequent sexual activity which encompasses all possible sex dyads. An important part of the bonobo social life goes indeed through the filter of their sexual activity, notably the famous female-female genital rubbing (Hohmann and Fruth 2000; Clay 2010; Clay et al. 2011).

**Cognition and communication**

While chimpanzee physical cognition is well developed (see above), bonobo physical cognition has been thought to be inferior and more limited (Helme et al. 2006). A more recent study, however, did not find any differences between all great apes in their understanding of the functional properties of tools (Herrmann et al. 2008). Additionally, the two species do not differ in significant ways in manipulation skills and motor sequences (Takeshita and Walraven 1996). Similarly to orangutans, bonobos have also been shown to save tools for future use (Mulcahy and Call 2006a). Thus, the most recent results appear to describe bonobos and chimpanzees as having comparable physical cognition.

Regarding social cognition, studies on chimpanzee have provided numerous examples that support the claim that animals can be deceptive (Byrne and Whiten 1988; Whiten and Byrne 1997). Recent laboratory studies have shown that chimpanzees understand many aspects of their social partners: they know what other know, even when they have to rely on inferences only (Hare et al. 2000; Kaminski et al. 2008; Schmelz et al. 2011); they understand goals and intentions as action plans (Call et al. 2004; Buttelmann et al. 2007); finally, they can conceal information from others (Hare et al. 2001; Melis et al. 2006).

More recently, however, there have been more studies with captive bonobos (Hare et al. 2007; Hare 2009). They generally match chimpanzees in most tasks, although interesting differences are also found. For instance, bonobos perform better on socially-related tasks while chimpanzees perform better on physically-related tasks when the two species are tested with the same battery of tests (Herrmann et al. 2010). Bonobos also outcompete chimpanzees in cooperative tasks, which is thought to result from their greater tolerance of conspecifics (Hare et al. 2007; but see Jaeggi et al. 2010b).

Chimpanzee and bonobo communication is multi-modal and has been investigated both in captivity and in the wild. As our closest relatives, findings about their communication systems allow us to study both animal vocalisations and the evolution of our own language (Zuberbühler 2006). Ape gestures present some characteristics of human language in that they have been shown to have a learnt part, are flexible, and require a directed connection between the signaller and the receiver. As such, they have been proposed to be at the evolutionary roots of human language, in contrast to vocalisations which have been described as genetically hardwired and less flexible (Call and Tomasello 2007; Arbib et al. 2008; Tomasello 2008). However, recent data on chimpanzee and bonobo vocalisations show that

flexibility is also present in their vocal behaviour. Both chimpanzees and bonobos adjust their vocal behaviour according to their audience and can use their vocalisations strategically (Slocombe and Zuberbuhler 2005; Slocombe and Zuberbühler 2007; Townsend et al. 2008; Clay 2010; Clay et al. 2011). In summary, even if the debate about the evolutionary origins of language is still ongoing, both camps have proved on numerous occasions that both bonobos and chimpanzees are very flexible in their communication, another aspect of their flexible mind.

### Tool use

More than any other behavioural trait, tool use has been considered as the major difference between bonobos and chimpanzees, as bonobos rarely use tools in the wild (e.g. McGrew 1998). In chapter 3, I will review and compare chimpanzee and bonobo tool use in the wild and in captivity to investigate if the difference in the wild data could result from a difference in their cognition. In chapters 6 and 7, I will connect this analysis with a study of Ugandan chimpanzee communities with low rates of tool use to investigate whether ecology could account for the differential use of tools between communities.

## 4. Summary

In this first part, I have presented tool use in animals and shown that it was found broadly in the animal kingdom, raising the possibility that it is the result of convergent evolution. I have also presented the numerous questions that are raised by these observations: how innate is tool use in animals? What do they understand about it? Data from birds, very interestingly, show that a strong genetic predisposition for tool use does not preclude flexibility. Finally, I presented the two species of interest in this thesis, the chimpanzee and the bonobo, who have many similarities but also differ strongly in their tool-using abilities.

In the second part of the introduction, I integrate tool use in the cultural debate, introduce the different controversies and show that much of the debate results from different philosophical stances.

# B. Animal culture: The current debate

## 1. Culture and social learning

### Insights from Koshima Island on the diffusion of animal behaviour

In 1953, the famous macaque Imo, one-and-a-half year old at the time, brought a sandy sweet potato provisioned by researchers to the water and washed the sand off it. This event could have remained an individual prowess, but over the following decade, the behaviour spread to most of the troop, so that by 1962, 36 out of 49 monkeys (73.4%) over two years old were displaying this behaviour. The spread of sweet potato washing was documented by Japanese researchers and published for the first time in English in 1965 (Kawai 1965). Subsequent analyses and descriptions of the technique as well as of other techniques and traditions developed by the monkeys of Koshima Island have been published since (Kawai et al. 1992; Watanabe 1994; Hirata et al. 2001). Among other findings, it was noticed that a sex bias was present during the apprenticeship, with females older than four years old able to learn the behaviour more easily than males of the same age. This bias was tentatively explained by the fact that four years old males usually move from the centre to the periphery of the troop, and are thus less exposed to the behaviour. Additionally, and although Imo died in 1972, the behaviour is still present at the sixth generation in Koshima (Hirata et al. 2001).

Japanese macaque sweet potato washing (SPW) soon became a textbook example of animal culture. Although subsequent researchers refrained from using the word culture, preferring terms like ‘pre-culture’ or ‘protoculture’ (Kawai 1965; Menzel et al. 1972; Watanabe 1994), early researchers such as Kenji Imanishi, who started the research at Koshima (de Waal 2001) or Jane Goodall (1973), did not see a problem in describing the behaviours they observed in wild macaques or chimpanzees, respectively, as ‘cultural’. In this respect, culture was seen as any behaviour that was learnt “through a nongenetic channel” in social groups (Imanishi 1952). A number of scientists however, notably evolutionary psychologists, claimed that these behaviours did not have much to do with human cultures and could be at best analogical to them (Tomasello 1990; Galef 1992). Visalberghi and Fragaszy (1990b)

showed in a series of experiments that naïve monkeys would spontaneously wash their dirty food in the water, raising doubt that any individual at Koshima actually learnt something from seeing Imo performing SPW. Additionally, Galef argued that the speed of diffusion within the group was not high enough to support a social diffusion and that a more parsimonious explanation was that each individual developed the behaviour on its own (Galef 1992). More generally, evolutionary psychologists such as Galef (Galef 1988, 1990, 1992) or Tomasello (Tomasello 1990, 1994) argued that the transmission of the behaviours observed either in Koshima or Gombe was most certainly not done through imitation and teaching, two mechanisms that they saw as landmarks of human culture. According to them, what was claimed to be cultural in animals at that stage had little to do with human cultures and behaviours such as chimpanzee tool uses were most likely transmitted through simpler social learning mechanisms such as stimulus enhancement or emulation, rather than through imitation (Tomasello 1996). In the next section, I summarise the research that has been done on social learning mechanisms in animals and humans.

**Variety of social learning mechanisms**

A number of authors have reviewed and summarised the learning mechanisms that are at work in animals, especially in primates (Whiten and Ham 1992; Tomasello and Call 1997; Byrne and Russon 1998; Whiten et al. 2004; Hoppitt and Laland 2008; Whiten et al. 2009). Although there is still debate on the definitions of certain mechanisms (for instance, emulation or imitation: Tomasello 1996; Byrne and Russon 1998), recent research appears to generally agree on the nomenclature of these mechanisms. Given Galef's and Tomasello's claims, the question of whether animals imitate has become central. Before the early nineties, sweet potato washing at Koshima Island was often assumed to be a prime example of animal imitation (Galef 1992). Similarly, chimpanzees were also seen as an imitative species since the work of the Hayes (Hayes and Hayes 1952). However, re-analysis of these data and new experiments conducted with monkeys (Visalberghi and Fragaszy 1990a) led researchers to doubt the reality of imitation in animals. Tomasello (1990) famously proposed that chimpanzee tool use could be explained by a mechanism that they named 'emulation' (after Wood 1989) and in which an individual learns about the function of an object by observing its conspecific using it, but re-invents the behaviour on its own, without copying the physical model. Most of the debate during the last two decades has therefore focused on determining if

any animal behaviour was in fact learnt through imitation at all (Byrne 1994; Byrne and Russon 1998). The last decades have seen a number of classifications be proposed, mainly to describe the social learning processes other than imitation that could account for the behavioural transmission observed in animals (Whiten and Ham 1992; Tomasello and Call 1997; Byrne and Russon 1998; Whiten et al. 2004; Whiten et al. 2009). When full-blown imitation would imply to both understand the goal of the other individual and replicate its behaviour, other mechanisms can only address parts of the problem (Table 1.1.).

Often believed to the 'cheapest' ways of acquiring information, 'local enhancement' and 'stimulus enhancement' (Spence 1937; Thorpe 1956), describe the "tendency to pay attention to, or aim responses towards a particular place or objects in the environment after observing a conspecific's actions at that place or in conjunction with those objects" (Byrne and Russon 1998, p. 669). The only influence of a conspecific on a naïve individual is thus to bring it to realise that something in its environment is interesting, but it has to work out what to do on its own. Following in terms of apparent complexity, a number of mechanisms such as 'observational conditioning' or 'affordance learning' (Whiten and Ham 1992; Whiten et al. 2004), get individuals to understand more about their environment, either through repeated exposure to a phenomenon or the physical properties of the object of interest. Different meanings have been attached to 'emulation' since its first proposal by Tomasello (1990). The primary 'goal-oriented' definition was expended to include 'affordances' of the tools and the understanding of working relationships between objects (Nagell et al. 1993; Call and Tomasello 1994).

**Table 1.1.** Summary of the main social learning mechanisms in animals (adapted from Whiten et al. 2004; Hoppitt and Laland 2008).

| Strategy | Characteristics | General definition |
|---|---|---|
| **Local or stimulus enhancement** | One individual's attention is inadvertently attracted by a conspecific's behaviour, but it develops on its own the particular behaviour | "Tendency to pay attention to, or aim responses towards a particular place or objects in the environment after observing a conspecific's actions at that place or in conjunction with those objects" [1] |
| **Observational conditioning** | One individual learns the value (positive or negative) of a stimulus by observing others' reaction to it | "Observation of a demonstrator exposes the observer to a relationship between stimuli at $t_1$, and exposure to this relationship effects a change in the observer detected, in any behaviour, at $t_2$" [2] |
| **Affordance learning** | One individual learns about the operational properties of objects by witnessing others or the environment acting on it | "Observational learning of physical properties of objects and of relationships among objects" [3] |
| **Emulation learning** | One individual learns about the functional properties of an object, without learning the behavioural means to achieve that goal | "The learner observes and understands a change of state in the world produced by the manipulations of another" [4] |
| **Imitation learning** | One individual learns both the function of a particular action and the way to proceed to achieve the goal of this action | "Through observing a demonstrator performing an action in a specific context, an observer becomes more likely to perform that action in the same context" (Contextual imitation) or "When after observing a demonstrator performing a novel action, or novel sequence, or a combination of actions that is not in its own repertoire, an observer then becomes more likely to perform that same action or sequence of actions" (Production imitation) [5] |

[1]: (Byrne and Russon 1998, p. 669); [2]: (Heyes 1994, p. 220); [3]: (Byrne 1998, p. 604-05); [4]: (Tomasello 1996, p. 321); [5]: (Hoppitt and Laland 2008, p. 109).

Imitation itself is controversial and numerous behaviours that are often claimed to be true imitation may only be the result of response facilitation (Byrne and Tomasello 1995). Byrne and Tomasello also claim that novelty is a prime criterion when deciding if a certain behaviour has truly been transmitted through imitation. Such condition appears to have been fulfilled during the recently observed transmission of the 'liana-scratching' behaviour performed by a maimed adult chimpanzee, apparently imitated by young able-bodied chimpanzees (Hobaiter and Byrne 2010). Another useful distinction introduced by Byrne (Byrne 2002) distinguishes the notions of contextual imitation and production imitation, based on the notions of contextual and production learning proposed by Janik and Slater (Janik and Slater 2000). Where production imitation or learning causes the learning of a novel behaviour that was not previously in the repertoire, contextual imitation allows one individual, after seeing a conspecific using a behaviour already part of their common repertoire but this time performed in a novel context, to copy this behaviour in the novel context. Interestingly, the major focus of this theory is not so much on the behaviour than on its contextual use. Contextual imitation thus focuses on the imitation of the context rather than on the imitation of the behaviour itself.

Finally, a second separation has been proposed by Byrne (1994) following his work on nettle processing in gorillas (Byrne and Byrne 1993). Imitation learning can consist of learning and reproducing the physical action of a behaviour (production level); however, for complex behaviours which require several steps, it can also consist of learning and reproducing each of these steps (programme level). An interesting point developed in programme-level imitation is that the content of each step on its own is not necessarily learnt through social learning; on the contrary, it can be learnt through individual trial-and-error learning (Byrne and Russon 1998). Such a theory thus allows its authors to build a bridge between individual and social learning during the acquisition process.

**Culture and traditions**

Culture is generally understood as encompassing any kinds of behaviours that are not individually acquired or innate. In essence, it is composed of behaviours that are at least in part socially acquired. These behaviours are named traditions, for which a globally accepted definition given by Fragaszy and Perry (2003a, p xiii) is "a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning". Many researchers, notably from biological sciences, have adopted the two words (culture and tradition) interchangeably (Laland and Galef 2009a). Some researchers, however, still dispute this idea, arguing for instance that the main characteristic of a tradition is that it is transmitted vertically between generations, but that it does not make it necessarily cultural *per se*. For instance, a particular way of making a cake in one family is a tradition within the family, but is most likely not shared by the rest of the population, thus, not cultural in the general sense of the term (McGrew 2004, 2009). Similar ideas are developed in the case of marine mammals: Shark Bay bottlenose dolphins have come to fame notably through the use of tools during hunting (Mann 2009); however, not all females in the population use tools, and most of the behavioural traits show, on the contrary, a strong familial structure, making them unlikely candidates for cultural variants, but nonetheless strong candidates for socially transmitted traditions (Mann and Sargeant 2003; Sargeant and Mann 2009).

Other authors have contested the idea that traditions are equivalent to culture and drew there a distinction between animal traditions and human cultures, with the latter necessarily relying on complex forms of social learning such as imitation and teaching (Galef 2009; Hill 2009). Perry and colleagues (Perry and Manson 2003; Perry 2009) insisted in their publications that although their observations proved the existence of traditions in wild capuchins, they would not consider them equivalent to human cultures, thus preferring the term 'traditions' rather than 'culture'. In recent review chapters, opinions have ranged from a complete acceptance of the term culture for many animal species (de Waal and Bonnie 2009) to a complete rejection of this term to describe the behavioural diversity observed in animals (Galef 2009; Hill 2009). The use of the word culture, after having been used freely by Jane Goodall or Kenji Imanishi, has often been abandoned under the pretext of carefulness and parsimony. Hirata and colleagues (2001, p. 490) summarise the problem as follow: "We must not overestimate the situation and say that "monkeys have culture," and then confuse it with human culture. Cultural behavior in monkeys must always be discussed in the light of evolution. This is the

reason why the term "preculture," which takes such differences in consideration, was used in Kawai's paper".

Finally, other studies have attempted to reconcile both terms. Aware that many species have only a few traditions at hand, and that they are mostly present within a unique context, Whiten and van Schaik (2007) have proposed that species should be granted with culture whenever they prove to have multiple traditions in many different domains (for instance food acquisition, social interactions or communication). This method can be criticised as it introduces the inevitable problem of determining where to put the threshold and to decide that a species has enough traditions in enough different domains to be granted culture. However, the current state of knowledge on animal traditions shows that only few species, notably great apes, show a large number of traditions spread in different contexts, making them prime candidates for the cultural label. Rather than granting this cultural label to any species that shows a transfer of information that is transmitted through nongenetic means (Lumsden and Wilson 1981), such a method helps to set a limiting condition that is not exclusively based on the transmission mechanisms, but also privileges the complexity of the general picture for a given species. For instance, birds show socially learned behaviours but mainly during song learning (e.g. Slater and Ince 1982; Slater et al. 1991; Catchpole and Slater 1995). Therefore, they would fall in the category of species that show socially learned behaviours but only in a limited domain, which would not grant them with the cultural label according to Whiten and van Schaik's definition.

Another approach that has been proposed is to examine the complexity of the behaviours that are presumed to be cultural. In this case, only behaviours of a certain complexity are unlikely to be re-invented several times; additionally, unlike the cake traditions mentioned above, they are likely to be near ubiquitously performed among a continuous population. The conjunction of these traits would make them cultural (Byrne 2007b).

In summary, although tradition is used commonly in the animal literature, authors less readily use the term culture, as its use is uncomfortably felt as having 'something more' than the more innocent 'tradition'. In the rest of this thesis, I will use culture and tradition interchangeably, as most commentators do. However, I acknowledge the fact that culture and traditions should not be confounded, and notably, that cultures are composed of traditions. In this respect, I follow Whiten and van Schaik (2007) in their distinction.

**Culture is composed of socially arbitrary conventions**

Animal cultures are not exclusively composed of tool-using behaviours. They also include social traditions. In a certain way, the presence of social traditions in a given species is a better proof of culture than tool-using behaviours, as they can be completely arbitrary, while tool-using behaviours have an adaptive value in that they help an individual to survive. For instance, in Taï, it is crucial for individuals to learn nut-cracking, as it is the major food source during the so-called "nut-cracking" season (Boesch and Boesch-Achermann 2000). On the other hand, social conventions can be completely arbitrary, and displaying them may not have any obvious advantages.

The first documented instance of a social custom in chimpanzees by McGrew and Tutin (1978), handclasp grooming (which consists in holding the hand of a grooming partner with one's own hand above both heads) illustrated the idea that certain behaviours with no apparent functions could be found in certain groups but not in others. This behaviour has been nowadays documented in a number of other communities, including in captivity, where it developed following the inclination of one particular female (de Waal and Seres 1997), but is still absent in some wild ones (Whiten et al. 1999). Such variation in social situations can also have a communicative purpose and may even include tools. As mentioned previously, the same tool-using behaviour, leaf-clipping, is used for different purposes in Budongo or Mahale on the one hand, and in Taï and Bossou on the other hand (Whiten et al. 2001). Other commonly cited behaviours are found in macaques, capuchins and orangutans.

Macaque stone handling is a behaviour for which the appearance and the spread have been very well documented in Japanese populations (Huffman 1984; Huffman and Quiatt 1986; Huffman 1996). While food-washing techniques could be seen as an adaptive answer to a change in the environment, the stone handling techniques that were first described in Arashiyama appeared as a seemingly non-adaptive play activity (Huffman 1984). Stone handling techniques stand for all kinds of behaviours which result in manipulating the stones in different ways such as pounding them against each other or against a hard surface, rolling or rubbing them, or simply carrying or throwing them (Huffman et al. 2008). After the initial description in Arashiyama, these behaviours were found in a number of different communities, and a total of 45 different behaviours have been described across 10 sites, a number of them being described as local variants because of their geographical repartition (Leca et al. 2007b).

In 2003, a collaboration between 10 researchers, involving 13 social groups of white-faced capuchins spread across four study sites and studied over 13 years, documented and compared the behavioural patterns from these groups (Perry et al. 2003a). They documented the appearance and disappearance of certain behaviours, and classified five behaviours as social traditions: hand sniffing, sucking of body parts, and three behaviours classified as "games". Contrary to the macaque groups described previously, the behaviours described in this study were mostly seen as interactions between individuals and as group or clique-specific social conventions. Certain behaviours indeed require to lower one's own safety, and may even represent some danger for one of the participants (e.g., letting one's finger between the other's teeth), thus, the primary function of these behaviours was proposed to be a means of assessing social relationships between individuals (Perry et al. 2003a).

In orangutans, a number of behaviours which are not food related but can either have a recreational or social purpose have been recorded as cultural variants (van Schaik et al. 2003; van Schaik et al. 2006; van Schaik et al. 2009a). This is particulary true in a number of sexual behaviours. Orangutans in certain sites use tools for sexual stimulation, while in others, males and females share the same nest during consortship. Particular vocalisations are also found in some communities and not in others, such as the 'throat scrape' produced by a mother towards her offspring. This last point illustrates also the difference between birds and orangutans if one adopts Whiten and van Schaik (2007)'s criterion: while birds' social learning is mostly limited to vocal learning, the particular 'throat scrape' vocal variant appears within a number of cultural variants that occur in domains as diverse as food acquisition or sex.

## 2. Different approaches to the study of culture and associated criticisms

### The 'ethnographic', 'geographic' or 'exclusion' method

Following earlier work by McGrew (McGrew 1992), Whiten and colleagues (1999) proposed a method, which has been known as the 'ethnographic' (Laland and Janik 2006), 'geographic' (van Schaik 2009) or 'exclusion' method (Krützen et al. 2007), to identify culture in animals through the comparison of different patterns of behaviours across sites. They illustrated this method with the data of seven long-term chimpanzee study sites. The idea they developed was that the behavioural differences observed between sites could be considered to have three possible origins: they could either have a genetic origin, and the differences in the genomes of genetically different populations would explain the observed differences at the phenotypic level; an ecological origin resulting from different environments (for instance nut-cracking cannot possibly develop in a nut-free environment); or a socio-cultural origin through socially learnt information. They identified a grand total of 65 behaviours across sites, found 42 that varied significantly across them, and isolated 39 of 42 for which they discarded ecological or genetic explanations, leaving the cultural hypothesis as the most parsimonious explanation. This suggested that the differences between the sites resulted from socially learnt processes, much like human culture (de Waal 1999). Soon the method was repeted in other species: orangutans (van Schaik et al. 2003), white-faced capuchins (Perry et al. 2003b, although these authors prefer the word 'traditions' to 'culture') and whales and dolphins (Rendell and Whitehead 2001), among others. However, concomitantly, critics of the method appeared. Similarly, older animal culture sceptics also adapted their criticisms to this new method as its use in the field became widespread. I will now describe these criticisms, which I have separated according to the field of origin of the authors who proposed them. This separation is also a chronological one, as psychological criticisms were the earliest and the anthropological ones the latest criticisms to be formulated. However, other than these two reasons, I should stress that these separations and this nomenclature are arbitrary in terms of content, in that criticisms proposed by psychologists can well have to do with biological problems.

**Psychological criticisms and answers**

I name psychological criticisms the criticisms that have mainly been formulated by evolutionary psychologists Michael Tomasello (Tomasello 1990, 1994) and Bennett Galef (Galef 1992). They are the oldest, historically speaking, and even though they were not originally formulated against the exclusion method, they were adapted to this method and are still maintained by their authors as of now (Galef 2009; Tomasello 2009). As described above, these criticisms are based around two major points. Firstly, they point out that there is no proof that animal tool use observed in the wild is the result of social learning. Rather, it could be that each individual re-develops the behaviour present in its community because of ecological constraints. Secondly, they claim that human culture is sustained through imitation and teaching, which they think are absent in nonhuman species. Concentrating their attacks against chimpanzee and macaque presumed cultures, they claim that even if social learning mechanisms are present in these species, they are not the same as in humans.

These claims have been largely addressed by researchers working with captive animals, who showed that a range of social learning mechanisms, including imitation, are available to chimpanzees and can successfully sustain the transmission of behaviours through 'virtual' generations (Whiten 1998; Horner and Whiten 2005; Hopper et al. 2007; Whiten et al. 2007). Whiten first showed that there was some evidence of imitation in a captive chimpanzee (Whiten 1998), and Whiten and colleagues showed that a range of social learning mechanisms, including imitation, were used by chimpanzees (Whiten et al. 2004; Horner and Whiten 2005). Subsequently, they adapted a method originally designed in birds studies, the two-action methodology (Palameta and Lefebvre 1985; Akins and Zentall 1996; Zentall 1996; Lefebvre et al. 1997), to primates (Byrne 2002). In this method, two individuals are taken from two different groups; they are then trained with a different method to solve the same task (both methods being equally efficient); finally they are released again in their respective groups. The apparatus to which they were trained is subsequently proposed to their group and the spread of the method of choice to solve the task is studied in each group. Using this methodology, Whiten and colleagues showed that traditions could be artificially created in captive chimpanzee groups and that these traditions would even be transmitted between groups (Bonnie et al. 2007; Whiten et al. 2007). Finally, they showed that conformity, a landmark of human culture, was also present in chimpanzees (Whiten et al. 2005).

Additionally, although intuitive, there is no proof that imitation and teaching actually are the main mechanisms involved in the transmission of cultural behaviours in humans and their contribution to culture, whether for its transmission or its maintenance, is unclear in general (Laland et al. 2009; Claidière and Sperber 2010). In parallel, it has been shown that simple behaviours can readily be transmitted through 'simpler' types of social mechanisms in humans, showing that all human cultural behaviours are not necessarily transmitted through imitation or teaching (Caldwell and Millen 2009).

**Biological criticisms and answers**

The second set of criticisms that I introduce originated mainly from biologists, thus their denomination as 'biological criticisms'. However, certain criticisms by Tomasello or Galef also enter this set of criticisms.

Following the publications of a number of studies adopting the exclusion method (Whiten et al. 1999; Rendell and Whitehead 2001; Perry et al. 2003b; van Schaik et al. 2003), critics of this method pointed out that it was flawed with a number of conceptual and methodological problems (Laland and Janik 2006, 2007). They argued that it is impossible to analyse each potential origin individually, as the environment is responsible for the selection of the most adaptive traits, and that factors most likely continuously interact with each other. The second major criticism was that all the ecological parameters could never all be identified, so that the ecological influence may never be fully excluded (Galef 2009; Tomasello 2009). Finally, Laland and Janik argued that as much as one third of the behavioural variants in Whiten and colleagues' study were found only in one subspecies of chimpanzees, *P. t. verus*, which is the most divergent subspecies of the three as illustrated above, making impossible to rule out completely that genetics were not involved in the behavioural differences altogether.

As of now, most proponents of the ethnographic method acknowledge the interconnection of the different factors (van Schaik 2009), and new studies have tried to identify the amount of variation of behaviours due to each of the factors (Möbius et al. 2008; Schöning et al. 2008) rather than trying to attribute the general variation to one origin in particular. Phylogenetic analyses have shown that the segregation of the genetics cannot explain the segregation of the cultural variants, supporting the idea that factors other than genetics had to be considered to explain the general variation observed in behaviour (Lycett et al. 2007; but see Langergraber

et al. 2010). Additionally, new statistical methods propose to quantify how much of the variation of a behaviour can be explained with individual learning and how much needs to be complemented with social learning (Kendal et al. 2009; Laland et al. 2009; Kendal et al. 2010). Finally, the general development of the study of social influences in the wild through the use of field experiments (Matsuzawa 1994; Biro et al. 2003; Reader and Biro 2010; van de Waal et al. 2010) will help to test the different hypotheses directly in the animals' real habitat (see below). In general, biological criticisms have led researchers to design research programmes carefully monitoring each factor so as to determine for which traits social variables have to be taken into account to explain the observed variation.

**Ethnographic criticisms and answers**

The most recent set of criticisms comes from the anthropological domain (Hill 2009; Perry 2009). They concern mainly the limitations of the presumed 'animal cultures' in comparison with human ones. Rather than attempting to find origins other than socio-cultural to the behaviours presumed to be comparable with human cultural traits, they point out that human cultural behaviours are simply far more than varying traits between sites, even if these traits have a social origin. They are behaviours to which populations attach a value, sometimes a norm, which can be reinforced by a law in an institutionalised society. Moreover, many of these behaviours are being used as flags of the community that displays them. Hill shows that although the material variation present in primates can be assimilated to one side of human culture, which he names "*Socially learned techniques, technology and environmental information*" (p. 275), they lack the most important parts, which are, according to him, "*Regulations of individual behaviour enforced by rewards and punishments (norms, conventions, institutions, laws*" and "*Symbolic means of reinforcing, and signalling adherence to, a specific rule system*" (p. 276-277). These two characteristics give human cultures their most fundamental trait for the humans who hold them: a meaning. Concomitantly, Hill argues that humans have developed particular cognitive mechanisms adapted for culture, adopting Tomasello's view (e.g. Tomasello 2006). Similarly, Perry explains that there is probably more to culture than "behavioral variation that owes its existence in part to social learning" (p. 259), which is, according to her, the main reason of the disdain of cultural anthropologists for the debate of animal culture. In her view, the definition of ethnic markers and the enforcement of social norms are critical, notably through

the "symbolic linkage between social learned traits and a strong sense of group identity" (p. 265). Furthermore, both authors outline that this may be the principal reason why social anthropologists do not pay much attention to the animal culture debate: they just do not believe that they are dealing with the same topic.

Although Hill and Perry's criticisms put them on the side of a strong human-based definition of culture, notably emphasised by the use of words such as 'symbolic' or 'institutions', their arguments must nonetheless be taken into account. It is true that in any human community, even the simplest behaviour will be described as 'the way we do things'. Adopting such a phrasing particularly shows the direct link between a certain way of doing something and the people who adopt this certain way of doing this particular thing. Given that it is impossible to ask a chimpanzee if she has similar thoughts about the behaviour she is practising, such questions will probably remain unanswered for wild animals. However, they may still be pointing to a fundamental difference between humans and other animals and approaches have to be designed to tackle these questions.

## 3. New methods in the study of culture in humans and animals

### A cognitive approach to the study of cultures in humans

Anthropology is a science in which early work dates back to the Greek historian Herodotus (2,500 BC), and which was generally established as a formal discipline in the middle of the XIX$^{th}$ century (Haviland et al. 2008). However, it was not before the middle and late XX$^{th}$ century that it became linked to its biological roots, notably with the inclusion of cultural evolution within the natural selection framework (Campbell 1965, 1975; Durham 1976; Cavalli-Sforza and Feldman 1981; Durham 1982; Boyd and Richerson 1985; Boehm 1996). From that point on, for a growing number of researchers, culture was no longer a mechanism separated from evolutionary history that could not be analysed within the framework of biological sciences, but a product of human evolutionary history that needed to be explained. As such, two concurrent and co-evolving systems of inheritances have to be considered if one wants to understand the complete picture of human evolution (Mesoudi et al. 2004; Whiten 2005). Linking natural selection and cultural evolution allowed researchers to study human cultures under the scope of evolution and to create a number of concepts such as gene-culture

co-evolution (Richerson and Boyd 2005). Additionally, it allowed scientists to adapt biological ideas to the cultural debate such as niche construction, where a species modifies its environment by its own actions, which, in return, impact on its selection (Odling-Smee et al. 1996; Laland et al. 2000; Odling-Smee et al. 2003). In this respect, humans are usually referred to as the species that has overcome its biological evolution to only vary within the cultural realm. However, a better view of the interaction between the two selective processes is probably formulated by the niche construction theory. The example of dairy farming is the most cited example of niche construction: dairy farming societies developed a tolerance for lactose as one of the enzymes which enables its digestion, the lactase, kept on being produced even during adulthood while this was not the case in non-dairy farming societies.

In general, the connections between culture and biology allowed researchers to combine many concepts that originated in the general biological framework into cultural studies. The study of culture has taken a strong cognitive turn over the last few decades, notably under the influence of evolutionary psychologists (Tomasello 1999, 2006). Numerous studies have explored the links between culture and cognition and still continue to do so, from the early studies of face emotion recognition to the finding of differences between cultures in spatial cognition or in the very human sense of mathematics (Markus and Kitayama 1991; Mesquita and Frijda 1992; Greenfield 1997; Kitayama et al. 2003; Haun et al. 2006b; Casasanto 2008; Dehaene et al. 2008). Even more interestingly, the investigation of such differences at the neural level has started, with the coupling of cultural difference studies with neuroimaging, and data that show correlations between cultural variants and brain activations have become available (Paulesu et al. 2000; Bolger et al. 2005; Chiao and Ambady 2007; Han and Northoff 2008). For instance, Chinese participants will differ from American participants when performing the same task related to the notions of self or community. Such new approaches open large avenues of research for cultural sciences.

**Field experiments in animals**

While it is possible to directly ask people how they feel about what they are doing, it is impossible to do so with animals. However, some clever experiments conducted with humans can be adapted to chimpanzees, when little or no verbal indication is given to the participants. Levinson and colleagues (1992; 2002) developed various tasks to study spatial representation where subjects are required to remember the order and the orientation in which some items

are placed. They are then brought to another table in which they are asked to replace identical items in the same order or orientation. Crucially, the tables are turned 180° or 90°, allowing researchers to study their subjects' frame of reference (the system of spatial coordinates that they are using to specify spatial relationships between objects). While most of Western societies use a relative frame of reference based on the self to describe these relationships (such as 'the knife is on the right of the plate' if one is looking at the particular instalment of the dinner table, Fig. 1.4), some cultures rely mainly on an absolute frame of reference, where the position of objects are recorded according to their position in the cardinal directions (East, West, North, South). Others can also rely on the positions of objects relative to themselves. In general, frameworks relative to the subject are named egocentric, while frameworks relative to the environment are named geocentric. Consequently, when brought to a table that has been turned 90°, people using a relative frame of reference will organise the items according to their self perception (left to right) while people using an absolute frame of reference will remember the objects according to their position in the cardinal map (Levinson et al. 2002). Such a paradigm has been adapted to apes and allowed researchers to show that all ape species as well as non-verbal infants were adopting a geocentric frame of reference, but that this preference was then overridden in humans by the age of 8 when the preference then matched the one favoured by one's culture and language (Haun et al. 2006b). The authors concluded that this was the proof of a cultural override in human spatial cognition.

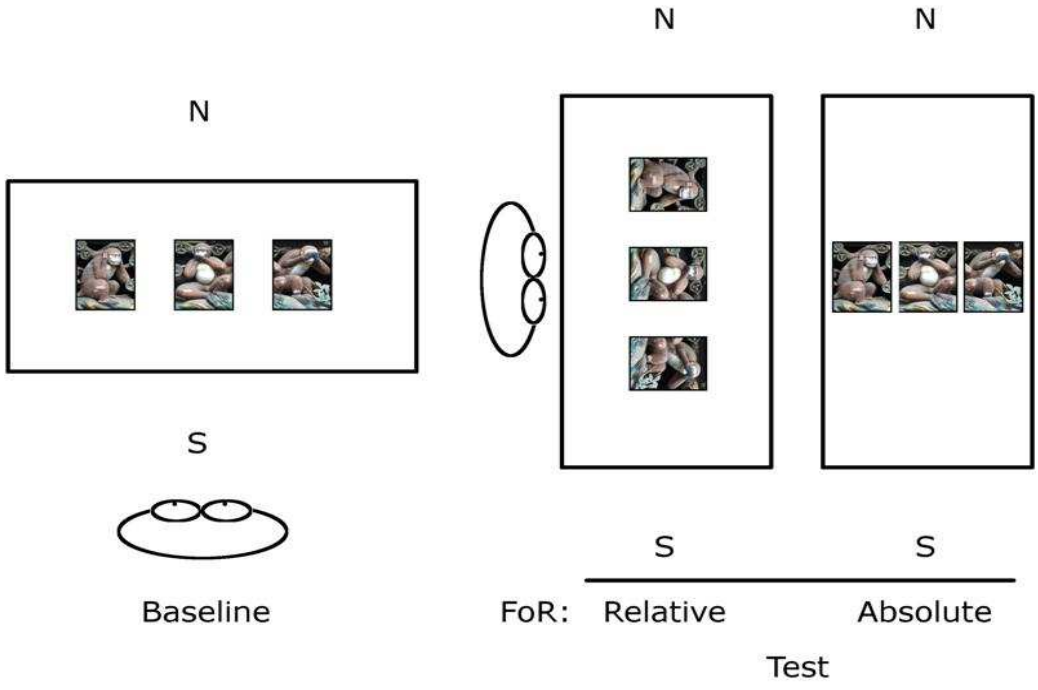


**Figure 1.4.** The 'turning table' paradigm showing the different frames of references (FoR).

It may seem unusual to start a paragraph about field experiments in animals with an experiment which is field-based with humans but laboratory-based with chimpanzees. However, I believe this kind of paradigm can be fully adapted to wild animals, as it requires very few verbal indication (none in the case of the captive chimpanzees, who only needed to understand that their task was to get the food reward) and allows individuals to express their preferences without having to follow some complex rules that would not be adaptable to chimpanzees. The key point about field experiments is that they have to be kept simple if one wishes to get some success. Reader and Biro (2010) recently published a review of field experiments that were conducted to assess social learning in the wild. The name 'field experiment' is self-explanatory, and consists in adapting the rigorous controlled experiments in captivity to field settings. Reader and Biro identified a total of 26 field experiments, in 20 different species ranging from fish to birds, exploring the role of social learning in various preferences such as feeding techniques, habitat choice or predator avoidance. 23 of 26 actually found proofs of social learning to a different extent, showing that social learning is widespread in animals and used in many different contexts. However, Reader and Biro documented only one study conducted with a primate species, the vervet monkey (van de Waal et al. 2010). Furthermore, they documented one study conducted with chimpanzees, which I am going to describe next, but which was not included in the list as the controls were not considered to be strong enough. Before that, however, the scarcity of studies conducted with chimpanzees should highlight the fact that what is easy to do with fishes can well be impossible to do with chimpanzees. For instance, translocation experiments, which consist in taking an individual from its native group and transporting it to another group, besides being extremely costly and dangerous as well as unethical in the case of an endangered species like the chimpanzee, would very likely fail as chimpanzees are extremely xenophobic and would probably end up killing the newcomer. Similarly, transporting an entire population from one site to another to study the influence of ecological variables is impossible with chimpanzees. Despite these logical difficulties, Matsuzawa and colleagues provided the much needed demonstration that field experiments could be implemented with chimpanzees.

Matsuzawa (1994) first described how a certain location in the Bossou forest was particularly suitable to become an "outdoor laboratory", as it was a clearing that chimpanzees crossed almost on a daily basis. Researchers provided nuts at this site, and chimpanzees soon came to understand that they could find them there, visiting more and more frequently to use their nut-cracking skills. The research team carefully monitored all available stones (weight and

size) to study which particular tool chimpanzees were selecting for nut-cracking and a number of developmental and ecological studies could be conducted (reviewed in Matsuzawa 1999). Finally, they provided different kinds of nuts and observed the reactions of the chimpanzees to them. Biro and colleagues (2003) noticed that, when introducing a certain type of nut, the coula nut, which is not present in the core area of the Bossou community, only one adult female, Yo, appeared to know of these nuts, and started to crack and eat them. The authors proposed the hypothesis that she had immigrated from another community which was used to eating them (Biro et al. 2003), which was confirmed by genetic analyses (Shimada et al. 2004). The exploration and the consuming of the nuts progressively developed in the group, notably as all juveniles became very interested in these nuts. Interestingly, the introduction of panda nuts, apparently unknown to the entire group, triggered much less interest from the community members. Thus, it seems likely that the presence of Yo influenced the other group members to engage with the coula nuts, for which they subsequently applied their knowledge of nut-cracking. However, in this case, it is hard to talk about the spread of behaviour, as it was already part of the community repertoire. Reader and Biro (2010), although acknowledging that the panda nut setting could in principle be the control for the coula nut setting, thus do not include this study in their survey because of a lack of control. The results of this study are nonetheless important and show how meaningful field experiments can be in the study of culture in chimpanzees.

## C. Summary and Outlook

"Well, in our country," said Alice, still panting a little, "you'd generally get to somewhere else — if you run very fast for a long time, as we've been doing."

"A slow sort of country!" said the Queen. "Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!"

Lewis Carroll, *Through the Looking-Glass, and what Alice found there*, (1871)

### 1. Summary: A problem of definition

In this last part of the introduction, I will summarise the major findings I described in the two first parts, and the conceptual and evolutionary consequences that they imply. I chose to present tool use independently from culture as I consider that the problems and the debates at stake are not of the same kind, and such an organisation allowed me to point out precisely what domains they encompassed. Now is the time to combine them together.

I started with a presentation of tool use and showed that, although it was first identified (or rather, confirmed) in chimpanzees by Jane Goodall in 1960, it is present in a great number of taxa. The presence of certain kinds of tool use in ants justly supports the question of whether it is similar to what is observed in humans. Because ants lack a brain, ant tool use is probably innate and does not include representations: thus it is possible that tool use in ants is not going to tell much about tool use in humans. However, birds are another enigma. Following Hunt's report of tool use in New-Caledonian crows (Hunt 1996), a number of questions that were first addressed with chimpanzees were subsequently addressed with birds. However, it is easier to test birds in captivity than chimpanzees, and notably to study the impact of social learning on the development of tool use. While chimpanzees will suffer greatly from social deprivation (Mason et al. 1968; Menzel et al. 1970), birds do not appear to experience such a problem, and Corbeau, who was raised in complete social isolation, developed tool use as fast as his conspecifics exposed to social influences (Kenward et al. 2006). However, this finding

does not mean that tool use in birds, although it includes a strong innate part, is not flexible. Emery and colleagues (e.g. Seed et al. 2006; Bird and Emery 2009a) have shown that such tool use was very flexible, raising the very interesting point that having a strong genetic predisposition for tool use does not preclude flexibility. This fact should be taken into account in the cultural debate, where too often a genetic component in tool use appears to be a no-go that would make animal tool use completely different from human tool use, while how much genetic human tool use actually is, is not even known. The approaches adopted by the researchers who are concerned about the cognitive properties and implications of tool use appear thus very interesting to integrate in the cultural debate.

Secondly, I presented the cultural debate and showed that although it is ancient and dates back to the initial Koshima observations, the problem is still the same. Old critics of the existence of animal culture are still critical of the recent findings, arguing that if social learning and preferably imitation, is not demonstrated by a very controlled experiment, then anything that can be brought by field researchers to sustain their claims of culture in wild animals will remain unconvincing. The proposal of a new methodology based on an ethnographic comparison of populations indeed does not provide much information about the mechanisms through which behaviours are acquired, as the method, as one of its names suggests, consists in excluding the other factors as unlikely to explain the observed variation in order to select most parsimoniously the one that remains. Critics of the method (e.g. Laland and Janik 2006) have soon pointed out that it was not conceptually possible to exclude one particular factor as all of them are likely to interact and influence the development of a behaviour in an individual. At the individual level, culture may indeed be the result of an interaction between genes and environment. At the population level, the very same factors may also be responsible for the observed variation. However, it may also be that when genes and environment are similar enough between some populations, the sole influence of culture could be isolated by comparing these populations. Subsequently, studies have aimed to quantify the level of variation that could be explained by each factor, rather than trying to exclude some of them. However, the most sceptics still argue, with reason, that we cannot exclude all ecological or genetic influences if we do not know to what extent genetics code for behaviours or are not able to identify all the subtle differences that can occur between sites. Somehow, from an external point of view, it seems that researchers of both camps are engaged in a Red Queen's race, where both have run a long way since the

1950s and the first observations of sweet potato washing at Koshima, but where the arguments of both sides still hold.

Concomitantly, though, research on human cultures has developed extensively, notably since psychologists have taken some interest in the cognitive foundations of cultural differences. I briefly described the new avenues of research combining culture and cognition in order to show that while research on animal culture seems to be a race run in the Queen's world, research in human culture on the contrary appears to go 'somewhere else', as rightly indicated by Alice. It would be very far from the truth to say that nothing has happened during the last sixty years, but the fact that the same old arguments can still be supported shows that they have not been addressed completely, and that if we do not succeed in addressing them, we will be stuck in a race that goes nowhere. An important contribution to the cultural debate has been made by anthropologists in their attempt to explain what is different between animal and human cultures (Hill 2009; Perry 2009). The very basic problem that we have to face is that researchers studying animal culture simply use a different definition than researchers studying human cultures. While the former agree to a definition of culture as a conglomerate of behaviours, namely traditions, for which a widely accepted definition is the one proposed by Fragaszy and Perry (2003a, p. xiii), on the other hand, the latter rely on a definition of culture as a conglomerate of ideas such as "a historically derived set of shared ideas, values, norms, and beliefs that underlie behavior" (Hill 2009, p. 279). Ideas are somehow frightening because they are not immediately grasped, and they need to be communicated by the other one to be understood. In other words, we have to rely on what other people say to infer what is in their mind. However, recent experiments show that very little communication is actually needed to understand a lot about how the mind works. Haun and Rapold (2009) showed how heavily frames of reference could impact on memory and covariate with different cultural backgrounds. Such an approach reveals how culture and cognition interact in the human mind, and is adaptable to chimpanzee studies. In this thesis, I will describe how to do so, and show that the results support the hypothesis that in chimpanzees, culture is also a matter of ideas as well as behaviours.

## 2. Outlook

This thesis presents the work that I have conducted in Uganda in two forests, the Budongo Forest Reserve and the Kibale forest in Kibale National Park, with several populations of

chimpanzees, most notably the Sonso community at Budongo and the Kanyawara community at Kibale. An interesting fact about the Sonso chimpanzees is that they are scarce tool-users (Reynolds 2005). Apart from a leaf technology, they virtually never use tools, a puzzle that I wished to investigate. However, on a larger scale, the Ugandan populations use fewer tools than other African populations (McGrew 2010), and the possibility to study in different sites in Uganda allowed me to investigate this tool use deficit within a more general picture.

I will introduce the Ugandan populations I have been working with and the methods that I have developed in the Methods chapter (chapter 2). In chapter 3, however, I will open the empirical work by presenting a study I conducted in a bonobo sanctuary in Democratic Republic of Congo (DRC), where I documented the tool-using abilities of the largest captive population of bonobos in the world. This chapter will give me the opportunity to analyse the role of genetics in tool use in the *Pan* genus and more generally to try to understand why bonobos in the wild are limited tool-users, which they are not in captivity. In chapters 4 and 5, I present different field experiments that I have been conducting in Uganda with the Sonso and Kanyawara communities. Firstly, I present the results of a field experiment, which aimed at developing a reliable way of assessing potential cultural variants isolated by the exclusion method. This study drives me to claim that chimpanzees rely on their cultural knowledge when they have to deal with novel tasks in their environment (chapter 4). Secondly, I present a follow-up study that aimed at analysing the cognitive components of tool-using in wild chimpanzees: how much they understand about a tool, what is salient for them, and generally how much their cultural knowledge actually influences their way of comprehending their environment (chapter 5). In chapter 6, I tackle the general question of why the Sonso chimpanzees do not use as many tools as their Kanyawara counterparts, and attempt to link the evolutionary history of the Ugandan forests with tool-using behaviours. Finally, in chapter 7, I discuss the implications of my work regarding tool use and culture in chimpanzees. I argue that these results are best explained by considering chimpanzee cultures as sets of ideas rather than sets of behaviours. By adopting this position, I show that the semantic problem between animal and human cultures disappears. More generally, this position brings human and chimpanzee cultures closer to each other while still allowing one to consider what truly differs between them.

# Chapter two: General methods

Parts of this chapter have been published in the method section of the following paper:

**Gruber, T.**, Muller, M.N., Strimling, P., Wrangham, R.W. & Zuberbühler, K. (2009) Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. Current Biology, 19(21): 1806-1810.

and are proposed for submission in the following paper:

**Gruber, T.,** Krupenye, C., Byrne, M.-R., Mackworth-Young, C. McGrew, W.C., Reynolds, V. & Zuberbühler, K. The influence of ecology on chimpanzee cultural behaviour. *Submitted.*

## Summary

In this chapter, I introduce the different communities I have been working with in Uganda. I present some of the ecological characteristics of the forests they inhabit, which I will study more thoroughly in chapter 6. Additionally, I introduce the Ngogo community of Kibale National Park which I did not study in person but that I include in a comparative study in chapter 6. I also introduce the experimental protocol of the field experiments I will present in chapters 4 and 5. Certain procedures will be described in their specific chapters. Finally, the methods used in the bonobo study will be described in chapter 3, along with the study itself.

### 1. Study sites in Uganda

My studies took place in Budongo Forest and Kibale National Park, which are home to the largest populations of chimpanzees in Uganda. Although they are now separated (distance camp to camp is around 180 km), these two forests used to be part of a continuous forest, which had originated from a core area in north-eastern DRC at the end of the last Ice Age, 12,500 years ago (Hamilton 1976; Grubb 1982; Howard 1991). Since then, the forests have generally retracted in recent times, mainly due to anthropogenic activities (Philipson 1977; Hamilton 1984; Hamilton et al. 1986; Howard 1991). The two forests have now been disconnected for 8,000 to 10,000 years (Reynolds 2005). During the Ice Age, most primate species stayed in a forest refugium somewhere in north-eastern DRC, from which they recolonised Uganda, following the growth of the forests (Goldberg 1996). Chimpanzees, however, are believed to have stayed outside of the refugium as a small population, resulting in very low diversity in current populations (Goldberg 1996; see chapter 6). Given that Budongo is one of the most north-eastern forests from the refugium, its composition in primate species is limited to the Eastern chimpanzee (*Pan troglodytes schweinfurthii*), the olive baboon (*Papio Anubis*), the black and white colobus monkey (*Colobus guereza occidentalis*), the blue monkey (*Cercopithecus mitis stuhlmannii*) and the redtail monkey (*Cercopithecus ascanius schmidti*). Additionally, vervet monkeys (*Cercopithecus aethiops*) are sometimes found in the forest but mainly range in the adjacent grasslands (Plumptre and Reynolds 1994). All these species plus L'hoest's monkey (*Cercopithecus lhoesti*), the red

colobus (*Pilocolobus badius*) and the grey-cheeked mangabey (*Lophocebus albigena*) are found in Kibale Forest, which is closer to the original refugium (Plumptre and Cox 2006). The two forests were logged extensively before, during and after the English colonial time. However, logging was more controlled in Budongo than in Kibale (Reynolds 2005), and an unexpected side effect was to favour the growth of fruit trees consumed by primate species (Plumptre 1996). My work in Sonso took place between January and March 2009 for a pilot study, then from September 2009 to October 2010 for a long-term study. In Kibale, I conducted a one month study in April 2009 and a one week study during August 2010.

I will now give some general information about the ecology of each forest. I will also describe the chimpanzee communities I have been working with, together with communities of interest that I will study in a general ecological comparison in chapter 6.

## 1.1. Budongo Forest

### General information about Budongo Forest

The Budongo Forest Reserve is located in western Uganda on the edge of the western Rift Valley, along Lake Albert (Latitude 1°37'-2°00'N; Longitude: 31°22'-31°46'E). The reserve encompasses 793 $km^2$ of moist semi-deciduous tropical grassland and forest of which 428 is forested (Eggeling 1947; Plumptre 1996). Eggeling (1947) and Plumptre (1996) delimit four main forest types, which follow in an ecological succession and intermix in frontier zones:

- A *Cynometra*-forest: the climax forest type dominated by *Cynometra alexandrii,* and which represents the ancient part of the forest.
- A mixed forest: dominated by *Celtis* subspecies and mahoganies.
- A colonising forest or woodland at the edge of the forest, dominated by *Maesopsis eminii* and *Cordia millenii*.
- Finally, a swamp forest along the streams containing notably *Raphia farinifera* and THV.

During British colonial time, a controlled extraction plan started in the 1930s attempted to suppress the climax forest part to foster the development of the mixed forest that contains highly valuable mahoganies. However, the most noticeable effect of this campaign that included selective logging and tree poisoning was the proliferation of fruit tree species

consumed by primates, notably numerous strangler figs species. Budongo Forest nowadays consists of three main blocks, separated by two roads and surrounded by several disconnected satellite forests and forest fragments (Plumptre 1996; Reynolds 2005; see Fig. 2.1). The forest is mostly flat and its mean elevation is of 1,100 m (1,084 m at Sonso camp site).

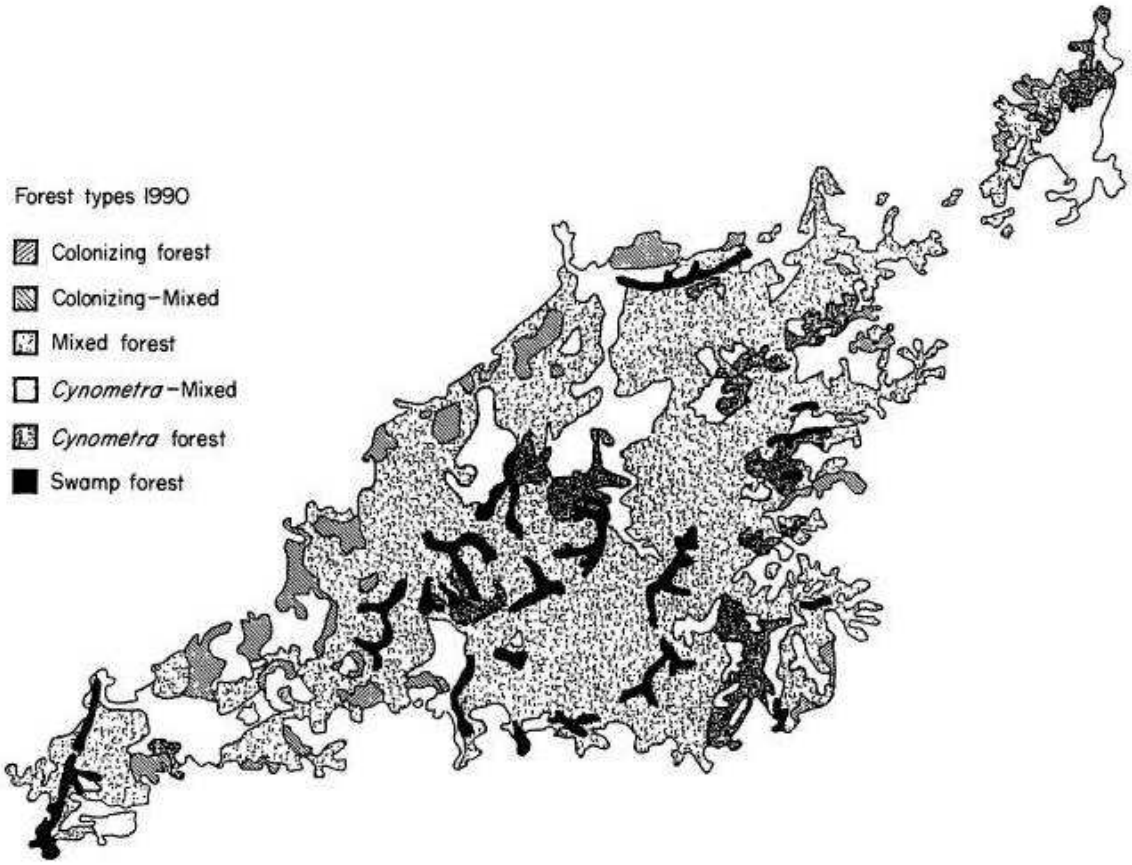


**Figure 2.1.** Forest types in Budongo Forest (courtesy of Andy Plumptre and Vernon Reynolds).

The entire forest contains approximately 640 chimpanzees, about 8-10 communities overall, with a density of 1.36 individual/km$^2$ (Plumptre et al. 2003). Additional communities live in the satellite forests surrounding the main forest block. Three communities living in the main forest block have been habituated partially or totally to human observers, at Busingiro, Sonso and Kaniyo Pabidi, where grid systems have been cut through the forest to allow the daily tracking of the chimpanzees (Fig. 2.2).

**The Sonso community**

Habituation of the Sonso community of Budongo Forest for research started in 1990, under the leadership of Prof. Vernon Reynolds. Most males and a number of females were fully habituated to human presence by 1994, when habituation was considered complete (Newton-Fisher 1999a). At the time of my study, some peripheral females remained defiant towards humans but core females were all as habituated as males.

At the beginning of the study, the Sonso community consisted of 73 individuals: 21 adult females, 20 adolescent females, and 11 infant females; 9 adult males, 8 adolescent males and 4 infant males. One infant was not sexed, two were born in the course of the study and 2 adults died from old age (TK) or because of a man-trap injury (SB, Table 2.1). The home range of the community is estimated to be around 6.78 $km^2$ (Newton-Fisher 2003).

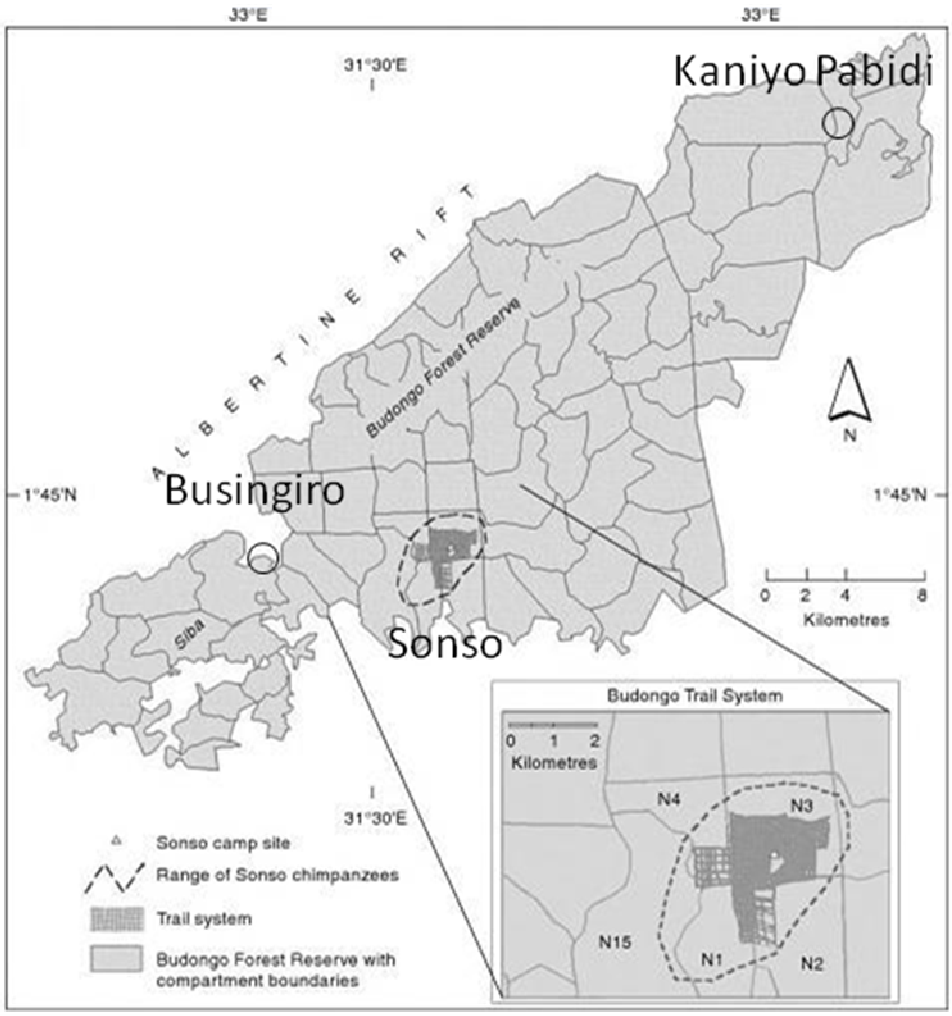


**Figure 2.2.** Map of the Budongo forest showing the location of Busingiro, Sonso and Kaniyo Pabidi (courtesy of Leela Hazzah and Mary Reuling).

**Table 2.1.** Members of the Sonso community at the beginning of the study (January 2009).

| Name | Code | Age (y) | Offspring | Code | Sex | Age (y) |
|---|---|---|---|---|---|---|
| Anna | AN | 19 | x | x | x | x |
| Beatrice | BC | 33 ± 5 | Squibs | SQ | M | 18 |
| | | | Birungi | BG | F | 5 |
| Flora | FL | 30 | Fred | FD | M | 15 |
| | | | Frank | FK | M | 10 |
| | | | Faida | FA | F | 3 |
| Gladys | GL | 33 ± 5 | Gina | GN | F | 13 |
| | | | Goria | GR | ? | 3 |
| Harriet | HT | 31 | Hawa | HW | M | 16 |
| | | | Helen | HL | F | 8 |
| | | | Honey | HY | F | 4 |
| | | | Heri | HE | F | b. Nov 09 |
| Janie | JN | 25 ± 1 | Janet | JT | F | 10 |
| | | | James | JS | M | 3 |
| Juliet | JL | 19 | infant killed by residing females | | | |
| Kalema | KL | 30 | Bahati* | BH | F | 15 |
| | | | Kumi | KM | F | 9 |
| | | | Klauce | KC | M | 3 |
| Kewaya | KY | 16 ± 1 | Katia | KA | F | 11 |
| | | | Kox | KX | F | 2 |
| Kigere | KG | 33 | Keti | KE | F | 11 |
| | | | Kuki | KI | F | 6 |
| | | | Kaspa | KP | M | 1 |
| Kutu | KT | 30 | Kato | KT | M | 16 |
| | | | Kana | KN | F | 11 |
| | | | Kasigwa | KS | M | 6 |
| | | | Kathy | KH | F | 1 |
| Kwera | KW | 28 | Kwezi | KZ | M | 14 |
| | | | Karo | KR | F | 8 |
| | | | Karibu | KB | F | 2 |
| Melissa | ML | 35 ± 5 | Monika | MN | F | 6 |
| | | | Mbotella | MB | M | b. Jan 09 |
| Mukwano | MK | 29 | Marion | MI | F | 3 |
| Nambi | NB | 47 | Musa | MS | M | 18 |
| | | | Nora* | NR | F | 13 |
| | | | Night | NT | F | 6 |
| Rachel | RE | 12 | x | x | x | x |
| Ruhara | RH | 44 ± 5 | Nick | NK | M | 17 |
| | | | Rose | RS | F | 12 |
| | | | Ramula | RM | F | 7 |
| | | | Rafia | RF | F | 2 |

Table 2.1. (continued)

| Name | Code | Age (y) | Offspring | Code | Sex | Age (y) |
|---|---|---|---|---|---|---|
| Sabrina # | SB | 28 | Sally | SA | F | 13 |
| | | | Sharlot | ST | F | 2 |
| Sarine | SE | 28 | Simon | SM | M | 16 |
| | | | Sokomoko | SK | F | 3 |
| Tanja | TJ | 25 ± 5 | Tapura | TP | F | 10 |
| | | | Tamara | TM | F | 5 |
| Verena | VR | 12 | x | x | x | x |
| Wilma | WL | 28 | infant deceased | | | |
| Zimba | ZM | 41 | Kewaya | KY | F | 26 |
| | | | Zig | ZG | M | 12 |
| | | | Zak | ZK | M | 7 |
| | | | | | | |
| Additional Males whose mother died or is unknown | | | | | | |
| Pascal | PS | 11 | | | | |
| Zalu | ZL | 14 | | | | |
| Zed | ZD | 8 | | | | |
| Zefa | ZF | 27 | | | | |
| Tinka # | TK | 49 ± 5 | | | | |

*: females who emigrated during the study; #: individuals who died during the study

**Other communities studied in Budongo Forest**

Two other communities have been habituated completely or tentatively in Budongo Forest. The Kaniyo Pabidi community has been partly habituated for eco-tourism but its current group size is unknown, although it is estimated to be similar to the Sonso community. At Busingiro, two communities of chimpanzees are found. One is estimated to be around 50 individuals, the other around 60 or 70. Even though chimpanzees were tolerant of human presence in the 1960s and allowed some studies to be conducted (Reynolds 1965; Sugiyama 1968), this was no longer the case at the time of my study. Kaniyo Pabidi is separated from the main block by the Masindi-Paraa road, and is located approximately 30 km from the Sonso site. Busingiro is found along the Masindi-Butiaba road and is located approximately 10 km from the Sonso site and 35 km from Kaniyo Pabidi.

## 1.2. Kibale National Park

### General information about Kibale National Park

The Kibale National Park is located in western Uganda, at the base of the Ruwenzori Mountains (latitude 0°13'-0°41'N; Longitude: 30°19'-30°32'E). The park is 795 $km^2$ large and consists of a patchwork of primary and secondary forest intermixed with grassland, swamp areas and exotic pine plantations (Chapman and Wrangham 1993). The forest is classified as moist evergreen or semi-deciduous forest transitional between lowland rainforest and montane forest (Struhsaker 1975, 1997) with dominant species including *Diospyros abyssinica*, *Markhamia platycalyx*, *Celtis durandii* and *Uvariopsis congensis* (Chapman and Wrangham 1993). Kibale Forest is hilly and altitude can vary between 1,350 m (Ngogo) and 1,500 m (Kanyawara). As a consequence, the variation in forest composition can be important between close sites and even within sites (Chapman et al. 1997; Potts et al. 2009; see chapter 6).

Kibale Forest contains about 1,400 chimpanzees, or 2.32 individuals/$km^2$, which is possibly the highest density of chimpanzees in Africa (Plumptre et al. 2003). Local densities at Kanyawara and Ngogo are 1.4 and 5.1 individuals/$km^2$, respectively. Most recently, the Kanyawara community counted 51 members, while the Ngogo community consisted of more than 150 individuals (Potts et al. in press). These two communities are separated by 12 km and are located about 180 km from the Sonso community of Budongo Forest (Fig. 2.3).

### The Kanyawara community

Although Isabirye-Basuta (1987) was the first to study the chimpanzees at Kanyawara between 1983 and 1985, habituation of the community for research was conducted from 1987 under the leadership of Prof. Richard Wrangham (Wrangham et al. 1991).

At the beginning of the study, the Kanyawara community consisted of 46 individuals: 14 adult females, 4 adolescent females, and 5 infant females; 10 adult males, 9 adolescent males and 4 infant males (Table 2.2). The home range of the community is estimated to be between 7.8 and 14.9 $km^2$ (Chapman and Wrangham 1993).

**Table 2.2.** Members of the Kanyawara community at the beginning of the study (April 2009).

| Name | Code | Age (y) | Offspring | Code | Sex | Age (y) |
|---|---|---|---|---|---|---|
| Bubbles | BL | 48 ± 5 | Budongo | BU | F | 12 |
| | | | Bono | BO | M | 6 |
| Ipassa | LS | 13 | x | x | x | x |
| Harare | HH | 16 | x | x | x | x |
| Kaana | JK | 17 | x | x | x | x |
| Lia | AL | 27 ± 5 | Tuke | AT | M | 10 |
| | | | Likizo | AZ | M | 5 |
| | | | Azania | AN | F | b. May 09 |
| Mususu | MU | 39 ± 5 | Max | MX | M | 11 |
| | | | Moon | MN | M | b. Dec 08 |
| Outamba | OU | 30 ± 5 | Tenkere | OT | F | 11 |
| | | | Tacugama | OG | M | 8 |
| | | | Omusisa | OM | F | 4 |
| | | | Gola | OL | F | b. Mar 09 |
| Quinto | QT | 17 ± 5 | Quiver | QV | M | b. Aug 08 |
| Rosa | LR | 20 | Obama | LO | M | 1 |
| Tongo | TG | 29 ± 5 | Lanjo | TJ | M | 14 |
| | | | Tuber | TT | M | 9 |
| | | | Tsunami | TS | F | 4 |
| Umbrella | UM | 28 ± 5 | Unasema | UN | M | 5 |
| Wangari | WA | 18 ± 5 | Wenka | WE | F | 2 |
| Wilma | WL | 17 ± 5 | Wallace | WC | M | b. Aug 08 |
| | | | | | | |
| Additional Females whose mother died or newly emigrating females | | | | | | |
| Euro | EU | 5 | | | | |
| Michelle | ML | 12 ± 5 | | | | |
| Rwanda | RD | 13 ± 5 | | | | |
| Special | NP | 9 | | | | |
| | | | | | | |
| Additional Males whose mother died or is unknown | | | | | | |
| Big Brown | BB | 43 + | | | | |
| Bud | PB | 14 | | | | |
| Eslom | ES | 15 ± 5 | | | | |
| Imoso | MS | 30 ± 5 | | | | |
| Johnny | AJ | 35 ± 5 | | | | |
| Kakama | KK | 24 | | | | |
| Makoku | LK | 27 ± 5 | | | | |
| Stout | ST | 54 + | | | | |
| Tofu | TU | 49 + | | | | |
| Twig | PG | 21 ± 5 | | | | |
| Yogi | YB | 36 + | | | | |

+: estimated error > 5 y

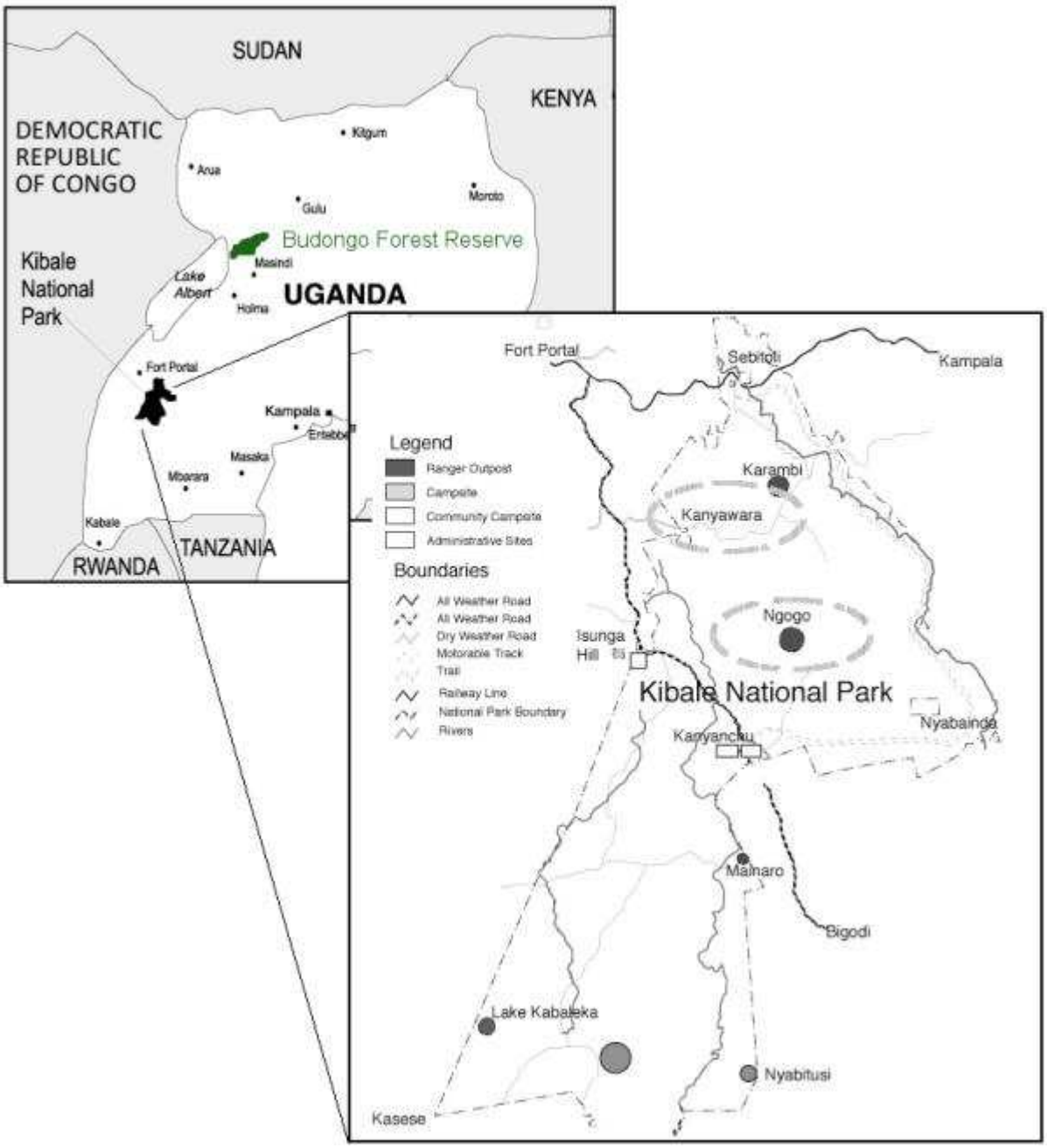


**Figure 2.3.** Map of Uganda with location of Kibale National Park and Budongo Forest Reserve with zoom on Kibale National Park showing the locations of Kanyawara and Ngogo (courtesy of Kevin N. Potts).

**Other community studied in Kibale National Park**

The Ngogo community was first studied by Ghiglieri (1984), but the first intensive research and habituation programme started with David Watts and John Mitani (e.g. Mitani and Watts

1999) in 1995 and continues nowadays. This community is the biggest ever observed in Africa, with approximately 150 individuals and notably around 25 adult males (Potts et al. in press). Some ecological factors, such as the high concentrations of protein in the mesocarp of ripe fruits, have been proposed to explain this unusually large group size (Mitani and Watts 1999; Hohmann et al. 2010). Although I did not directly study this community, I review some ecological data from this community for a comparative purpose in chapter 6.

## 2. Field experiments general protocol

### General protocol: The honey-trap experiments

Field experiments attempt to bring the controlled settings of the laboratory into the field. The experiments I conducted all aimed to study how chimpanzees would attempt to retrieve honey, a valuable natural food for chimpanzees in general (Boesch and Boesch 1990; Brewer and McGrew 1990; Bermejo and Illera 1999; Sanz and Morgan 2007), and in Budongo in particular (Reynolds 2005; Crockford, personal communication).

The apparatus I used was a simple hole drilled into a horizontal fallen log. This hole was 4x5 cm wide and of varying depths in order to study spontaneous or constrained tool use in wild chimpanzees (see chapter 4). The surface of the hole allowed adult chimpanzees to fit up to two fingers in the hole. Infants and young juveniles could fit their entire hand in the hole.

In order to control for ecological settings in the comparison between communities, I implemented the experiment in similar areas in Sonso and Kanyawara. In my first set of experiments (chapter 4), there was only one experimental location. At Sonso, the hole was drilled into a *Cleistopholis patens* tree that had fallen recently. At Kanyawara, the hole was drilled into a *Strychnos mitis* tree that had also fallen recently. At both sites, the tree fall had generated a relatively open area of about 25 $m^2$, surrounded by thick vegetation (Fig. 2.4). Twigs, climbers, and leaves were available as potential raw material for tools in large quantities at both sites. At Sonso, the log was located next to a *Raphia farinifera* tree where chimpanzees often came to feed (Reynolds et al. 2009). The site was usually visited by small subgroups that also used the place as a resting area. At Kanyawara, the log was located 30 m from a fruiting *Aningeria altissima* tree, in a cleared area where chimpanzees usually came

for grooming and resting after feeding. Both situations were similar in that there were no particularly interesting objects in the vicinity that might have prevented them from exploring the environment.

Every morning of an experimental session, I poured honey in the hole. All experiments were set up in the absence of chimpanzees. Access to the honey spot was unrestricted, and I did not interact with chimpanzees to attempt to attract them to the hole or to encourage them to engage with it. After setting up the experiment, I always left the area, and only came back if, while following a group of chimpanzees on their daily ranging, they returned to the site.


**Figure 2.4.** Experimental settings at Budongo (a) and Kibale (b) (pictures by T. Gruber).

**The portable logs**

In my second set of experiments (chapter 5), I replaced the massive fallen logs by standardised portable logs manufactured from dead logs collected in the forest. Various species (including *Albizia*, *Futumia*, *Broussonetia* and *Ficus* genera) were used as long as they were tender enough to drill a hole in them but solid enough to resist chimpanzees' strength and biting. Each log was standardised to a length of 50 cm, and a diameter of 25 cm. The 4x5 cm hole was drilled in the centre of each log. This technology allowed me to move the experiments to places where chimpanzees were foraging most often and to multiply the experimental locations in Sonso. This was indeed necessary as the Sonso chimpanzees did not engage with the experiment as much as the Kanyawara chimpanzees because many of them remained unsuccessful in obtaining honey (Fig. 2.5). The experimental set of data in Kanyawara was acquired in a single location near a fruiting *Ficus natalensis* that chimpanzees had started to visit the day before the experiment was implemented (Fig. 2.6). In Sonso, the logs were installed under fruiting trees often visited by chimpanzees, especially *Ficus sur* trees, which are a favourite chimpanzee food tree at Sonso (Newton-Fisher 1999), or on frequently used pathways. They were blocked under trunks and logs gathered in the vicinity to prevent chimpanzees from rolling them or attempting to carry them away (see Appendix E for pictures of the logs in the different conditions described in chapter 5).

**Honey acquisition and health and hygiene concerns**

Natural honey was acquired from local bee farmers of the Masindi District, Uganda, whose bees of the genus *Apis* forage freely in Budongo Forest. In order to limit the possible spread of potentially lethal diseases from humans to chimpanzees, notably respiratory, I only acquired honey from farmers whose practices were known and approved by the government (Uganda Natural Bureau of Standards) and honey was always collected under the surveillance of my field assistant. Farmers were required to wear protective masks and sterile gloves when handling honey or honeycombs. No additional operation (e.g., filtering) other than direct transport from the bee hive to a sealed bucket was allowed to be performed on the honey. Finally, it is noteworthy to mention that the natural antibiotic properties of honey also limit the risk of it carrying diseases.

**Chimpanzee exposure and ethical considerations regarding provisioning**

The first sets of experiments were conducted at Sonso between February 20 and March 25, 2009 and at Kanyawara between April 2 and 22, 2009. During these two periods, I poured honey in the hole every morning. The amount of honey provided each day was approximately of 100 ml. Following honey consumption by individuals, I monitored their health either by following them or by consulting field assistants and other researchers. No chimpanzee was ever reported to experience health problems after honey ingestion.

During the second set of experiments, given that I multiplied the number of experimental locations to multiply chimpanzee exposure to the experiment at Sonso, it was decided in coordination with BCFS scientific and field directors that exposure would be limited to one week maximum per location, with a minimum of two weeks break between two consecutive sets of experiments. Additionally, I conducted blank control tests to make sure chimpanzees were not associating the presence of honey with myself. For instance, I was standing with my camera as if in an experimental location, and studied if chimpanzees would modify their behaviour and start searching for honey. No individual ever modified its behaviour, showing that chimpanzees did not associate me with honey. Subsequently, in Kanyawara, the second set of exposure was also designed to be of one week.

I believe that the most problematic side to provisioning is that it drives chimpanzees to associate the food provided with humans. This can potentially generate problems with neighbouring human populations if it triggers chimpanzees to raid crops more and more frequently. However, in all my experiments, I made sure that chimpanzees did not associate me with honey as described above. Secondly, I provided food that is naturally present in their environment, limiting the risks that chimpanzees would make the connection to humans in general. Although the honey I used was acquired from farmers, chimpanzees did not modify their habits towards humans, suggesting that they did not notice that the honey had been first collected and handled by humans.

**Video recording of experiments**

In experimental sites, I positioned a motion-sensitive video camera PixController DVREye to survey the hole and the immediate area (20 $m^2$, see Appendix A). I also recorded additional video footages when possible with Canon FS100 and Canon FS200 Legria handy cameras.

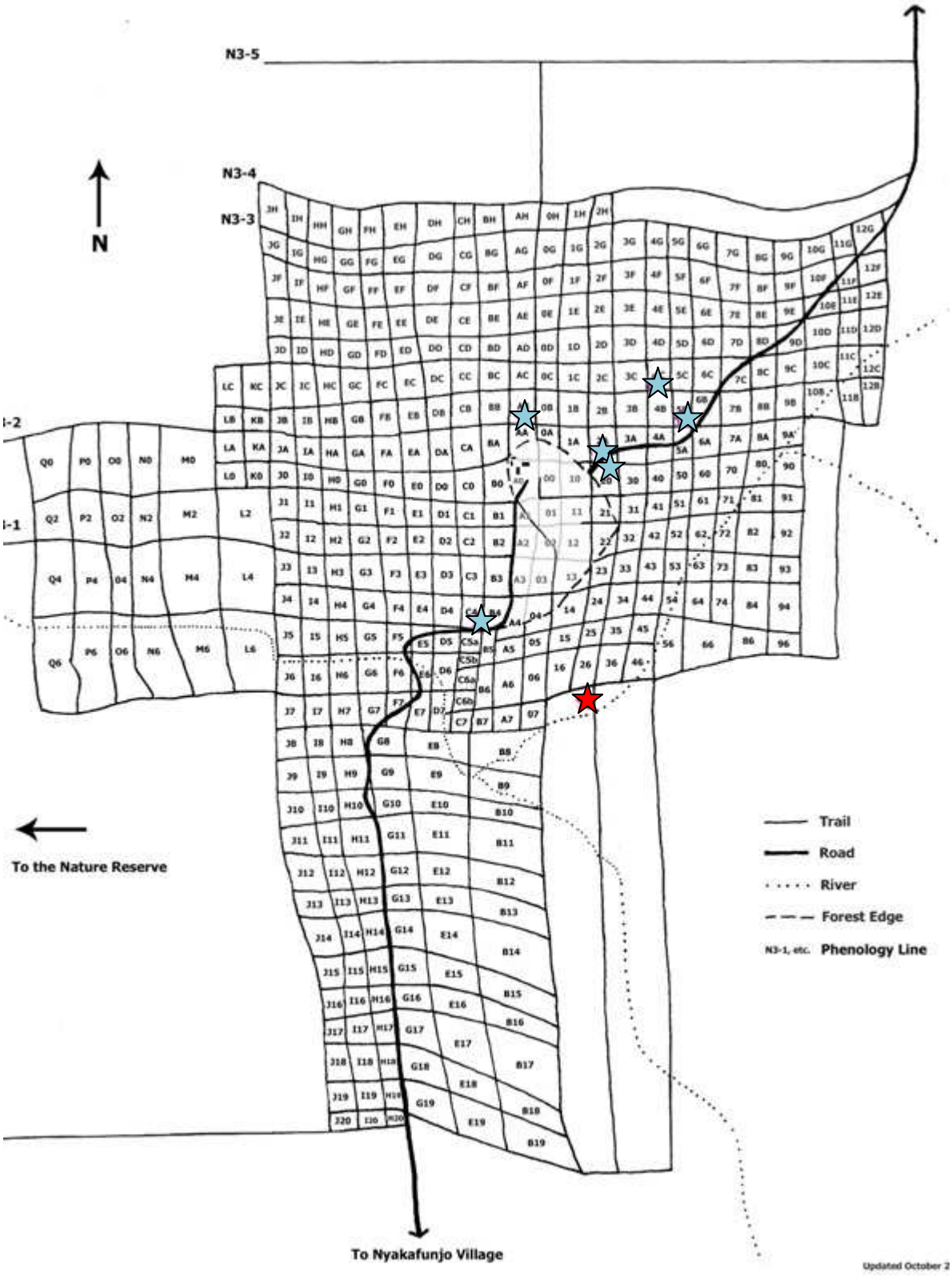


**Figure 2.5.** Localisation of experiments in the Sonso community grid system (Red: 1st set of experiments, chapter 4; Blue: 2nd set of experiments, chapter 5; Grid, courtesy of BCFS).

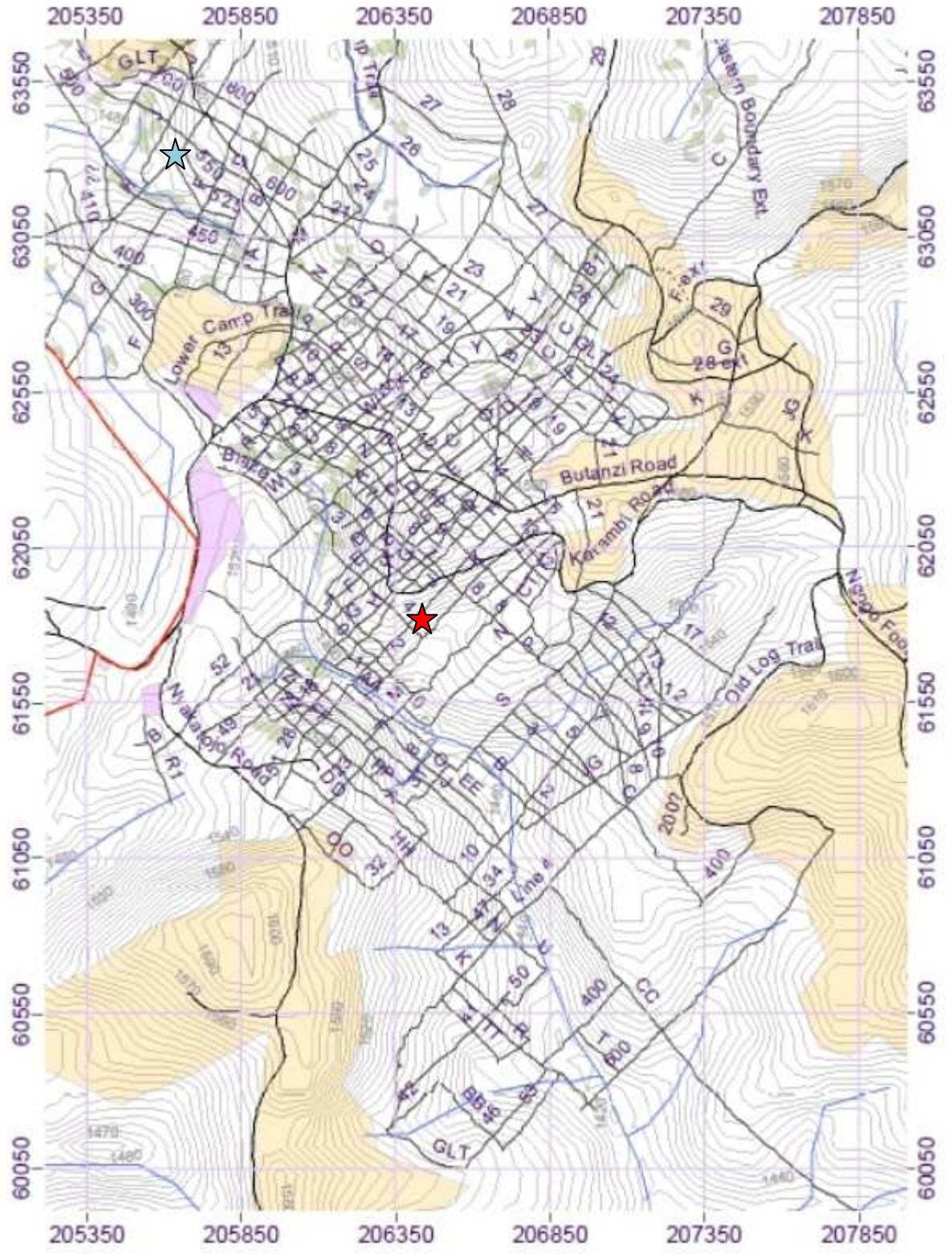


**Figure 2.6.** Localisation of experiments in the Kanyawara community grid system (Red: 1st set of experiments, chapter 4; Blue: 2nd set of experiments, chapter 5; Detail of the grid system, courtesy of Paco Bertolani).

# Chapter three: Bonobos and chimpanzees do not differ in their tool-using abilities

Results from this study have been published in:

**Gruber, T.**, Clay, Z. & Zuberbühler, K. (2010) A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. Animal Behaviour, 80(6): 1023-1033.

## Summary

Chimpanzees are the most sophisticated tool-users amongst all non-human primates. From an evolutionary perspective, it is therefore puzzling that the tool use behaviour of their closest living primate relative, the bonobo, has been described as particularly poor. However, only a small number of bonobo groups have been studied in the wild and only over comparably short periods, suggesting that this apparent difference may be due to an observational bias and may not reflect the reality. Here, I show that captive bonobos and chimpanzees are equally diverse tool-users in most contexts. I also provide observations which demonstrate that tool use in bonobos can be highly complex and no different from that which has been described for chimpanzees. An interesting difference, however, is that bonobos of all age-sex classes use tools during play behaviour, in contrast with adult chimpanzees who are rarely engaging in play behaviours at all. This behavioural trait should be related to the growing literature that describes the neotenous nature of bonobos in comparison to chimpanzees. A second highlight of the study is that female bonobos display a larger range of tool-using behaviours than males, a pattern that has been described in chimpanzees but not in other great apes. Thus, these data are consistent with the hypothesis that female-biased tool use evolved prior to the split between bonobos and chimpanzees. I discuss the potential evolutionary implications of this finding in light of the evolution of great apes and human cultures.

## 1. Introduction

Chimpanzees and bonobos are particularly interesting to study in a comparative perspective because they share a common evolutionary history until very recently and are our closest living relatives. Their current phenotypic similarities and differences have been the cause of much debate (Stanford 1998; Wrangham and Pilbeam 2001). One particularly relevant topic concerns tool use. Wild chimpanzees have shown a notable array of population-specific tool use behaviours (Goodall 1986; Whiten et al. 1999), a manifestation of their "material culture" (McGrew 1992). Only a small number of comparable observations of bonobo tool use have been made in the wild (Kano 1982; Ingmanson 1996; Hohmann and Fruth 2003a), suggesting that bonobos might differ from chimpanzees and humans in this fundamental way (McGrew 1998).

However, a number of isolated reports have described captive bonobos as rather skilful tool-users (Jordan 1982; Toth et al. 1993; Gold 2002). Additionally, the two species do not differ in significant ways in terms of manipulation skills and motor sequences (Takeshita and Walraven 1996). As described in chapter 1, interpretations of bonobos' underlying cognitive abilities are contradictory. One study claims that their tool-using behaviours are not based on a profound understanding of physical causation (Helme et al. 2006), while chimpanzees are believed to have a certain understanding of causal relationships (Limongelli et al. 1995; Mulcahy and Call 2006b; Seed et al. 2009a). However, bonobos, similarly to orangutans, save tools for future use (Mulcahy and Call 2006a) and a more recent report concludes that captive bonobos have the same understanding of the functional properties of tools as all other great apes (Herrmann et al. 2008). Thus, the most recent results appear to describe bonobos as having equal tool-using capabilities as chimpanzees.

Reports from the wild on bonobo and chimpanzee tool use also suggest a potentially interesting pattern. In terms of context, chimpanzee tool use occurs mostly during feeding and accession of difficult foods, such as hard-shelled fruits or concealed insects (McGrew 1992). In contrast, bonobo tool use has been observed mainly in social situations, such as in communicative contexts or play, but also during cleaning or to protect oneself from rain (Ingmanson 1996), a pattern also seen in captivity (de Waal 1986). At present, however, it is not possible to draw any firm conclusion about a potential difference in contextual use of tool-using behaviours between the two species. Chimpanzees are well known for their group-

and population-specific behavioural differences (e.g. Whiten et al. 1999; Crockford et al. 2004). The small number of studied communities of bonobos and the difficulties of obtaining data from the wild may however be responsible for the reported species differences in the wild. For instance, the most extensive study of chimpanzee culture is based on long-term data from seven different field sites (Whiten et al. 1999) while comparable data for bonobos is only from two sites (Hohmann and Fruth 2003a). Crucially, some chimpanzee groups hardly use tools in the wild, despite decades of long-term observations (Reynolds 2005). Thus, the limited tool use observed in bonobos may result from the fact that the communities currently studied are themselves limited in their tool-using repertoire, which may be due to ecological reasons (see chapter 6 for a discussion of the impact of ecology on the maintenance of tool-using behaviours in wild chimpanzees and chapter 7 for related predictions on bonobos).

Another interesting characteristic found by long-term studies with chimpanzees is that females are more accomplished tool-users during food acquisition than males, a fact with some implications for theories of human evolution (McGrew 1979; Marlowe 2005; Byrne 2007a; Pruetz and Bertolani 2007). So far, no comparable findings have been reported for bonobos, possibly due to the lack of observations in the wild. It is therefore unknown whether the female bias seen in chimpanzees is a species-specific peculiarity or whether it is present in both species, thus likely present in their common ancestor.

In this study, I compared the tool-using behaviours of captive chimpanzees and bonobos at various sites. For captive chimpanzees, I relied on the extensive catalogue compiled by Beck (1980), which I complemented with more recent data. For bonobos, I combined the published record (Savage, 1976 as quoted in Beck, 1980, Jordan 1982; Gold 2002) with data collected from three groups at San Diego Zoo (USA), San Diego Wild Animal Park (USA) and Lola ya Bonobo Sanctuary (DRC). I also used data from Twycross Zoo (UK) collected by another observer (Z.C.) following the same protocol. Given these data, I generated the most extensive tool catalogue in captive bonobos to date, and subsequently compared it with the chimpanzee catalogue. Additionally, I was able to analyse particular features of bonobo tool use such as potential sex differences in tool use, the presence of idiosyncratic tool behaviours, or the extent of tool use flexibility in these species, and compared them with long known facts about chimpanzee tool use.

## 2. Methods

### Subjects

I collected data from three different bonobo groups, housed at three different locations: San Diego Zoo (USA), San Diego Wild Animal Park (USA), Lola ya Bonobo (Kinshasa, DR Congo). During this study, I was assisted by another observer (Z.C.) who independently collected data following the same protocol in the group I was not working with (San Diego Zoo vs. Wild Animal Park) or with a different individual than the one I was observing (Lola ya Bonobo). Additionally, Z.C. collected tool-using observational data in the Twycross Zoo (2 groups) that I included in the final analysis to reach a total number of five different bonobo groups housed at four different locations. Group sizes ranged from 5 to 22. Age class categories were derived from Goodall (1986) simplified to four stages: infants (0-5 years), juveniles (childhood to early adolescence; male: 5-12, females: 5-10), sub-adults (late adolescence; male: 13-15, females: 11-13) and adults. Individuals were considered adults if they were either fully-grown or if they had given birth. All bonobos were able to witness the tool use behaviour of humans on numerous occasions and interactions with human caretakers were not uncommon. This was particularly true at Lola ya Bonobo where caretakers feed them daily using plastic bottles and demonstrated individuals from a young age how to break open nuts.

### Study sites

*San Diego Zoo*

Data were collected from the bonobos at San Diego Zoo between January and April 2008 with permission from the Animal Care Management at San Diego Zoo following approval by its IUCAC committee. The group consisted of three adult females, two adult males, one sub-adult female, one juvenile male and one juvenile female. The group was housed in a 560 $m^2$ outdoor area, connected to a heated indoor housing facility, which consisted of one large room (136 $m^2$) and four smaller rooms (55 $m^2$ each), which also served as sleeping areas at night. Individuals were unable to pass between the indoor and outdoor enclosures during the day. The composition of the Zoo group was managed with an attempt to simulate a fission–

fusion social system. Individuals were usually fed in a group setting three to four times per day, both indoors and outdoors, with a diet of roughly equal proportions of ape biscuits and cereals, vegetables, green leaf vegetables and fruits (approximately 25 types of foods per week). Water was freely available. Individuals were also given additional enrichment feeds (such as ice lollies and seeds) several times per week. An artificial termite mound in the outdoor enclosure, filled daily with honey and human baby food, provided additional enrichment.

*San Diego Wild Animal Park*

Data were collected at San Diego Wild Animal Park between January and April 2008, with permission from the Animal Care Management at San Diego Wild Animal Park and approval by its IUCAC committee. The group consisted of three adult females, three adult males, one sub-adult female and one juvenile female. The group was housed in an approximately 3,000 $m^2$ outdoor area, connected to a heated indoor housing facility, which consisted of one large room (47 $m^2$) and four smaller rooms (40 $m^2$ each) serving as sleeping areas at night. Individuals were unable to pass between the indoor and outdoor enclosures during the day. The group spent the entire observation time together. Individuals were usually fed in a group setting three to four times per day, both indoors and outdoors, with a diet of roughly equal proportions of ape biscuits and cereals, vegetables, green leaf vegetables and fruits, approximately 25 different types of food per week. Water was freely available. Individuals were also given separate supplementary enrichment feeds (such as ice lollies and seeds) several times per week.

*Lola ya Bonobo*

I collected data at the Lola ya Bonobo sanctuary in Kinshasa in September 2008. Z.C. collected additional observations between October and November 2008 and between August and November 2009 during a second visit. The study was conducted with permission from 'Les Amis des Bonobos du Congo' (ABC) Scientific Committee and its Scientific Coordinator. Lola ya Bonobo is a facility for orphan bonobos usually seized from the bush-meat and pet trade. All data were collected in 'Group 1', which consisted of six adult females, three sub-adult females, three adult males, three sub-adult males and three juvenile

males. Four infants were also present but their interactions with tools were not taken into account. The group was housed in a 10 ha outdoor enclosure during the day and in a subdivided indoor facility at night. Observations were conducted only when bonobos were visible in the open, non-forested areas of the enclosure (along the perimeter of the enclosures; approximately 15% of the total enclosure area). Despite this relatively small area, the bonobos spent a majority of their time on it (50-60% of daytime, Clay 2010) mainly because food was provisioned there. However, I cannot rule out that other tool use took place in the forested areas where observations were not possible. Individuals were fed a seasonal selection of fruits in the morning and vegetables in the afternoon, approximately 6 kg per individual per day, as a scatter feed to the entire group. At midday, bonobos were provided soy drink, enriched with honey, maize and vitamins, by a caregiver using a bottle. Additional enrichment food, such as bananas, peanuts and seasonal fruits, were provided once or twice per day. Bonobos had access to water from lakes and streams during the day. In addition to edible enrichment, bonobos were given enrichment items, such as plastic bottles and fruit shells, and they had free access to the large forested areas.

*Twycross Zoo*

A fourth set of data was collected by Z.C. at Twycross Zoo from March to July 2009 from two separate groups, following approval from the Twycross Zoo Research Coordinator and Zoo Management Committee and in compliance with the ethical guidelines set out by the British and Irish Association of Zoos and Aquariums (BIAZA). The first group consisted of two adult males, two adult females and one sub-adult female. The second group consisted of three adult females, one adult male, one sub-adult male and one juvenile female. The two groups were housed separately in one indoor building (124 $m^2$) composed of two identically designed heated indoor facilities. On each side of the building, the housing facilities for each group composed of one main 'day room' (62 $m^2$) and three off-show 'feeding rooms' (22 $m^2$). The two bonobo groups shared the outdoor enclosure (588 $m^2$) through temporal separation, with one group typically having access in the morning, and the other one in the afternoon. Both groups were fed a range of fruits and vegetables twice per day (typically four types of fruits and six to nine types of vegetables) in a scatter feed in either their outdoor or indoor enclosure. Water was freely available; milk and cordial were provided several times per day. In addition, bonobos received regular enrichment feeds, such as seeds or frozen juice

blocks, as well as access to a diverse array of edible branches and enrichment materials (some edible, such as seed boxes and some inedible, such as clothing/papers). Once or twice per week, bonobos were also provided additional feeds of live yoghurt, egg, cheese and bread. In both groups, an artificial termite mound was present in the indoor enclosure, although they were not used during the time of this study.

**Data collection and compilation**

At all four facilities, tool-using occurrences were recorded on an *ad libitum* basis during focal animal observations (Altmann 1974). At Lola, observation time was balanced across individuals (each day, one individual was selected and followed from 8 am to 4:30 pm), so that I could conduct systematic comparisons between them. At San Diego Zoo, San Diego Wild Animal Park and Twycross Zoo, observation time was unequal and I only used the data collected in these three sites to complete the tool use catalogue, where I combined the new data with already published records (Savage 1976; Jordan 1982; Gold 2002). I compiled data for wild bonobos from the published records (Ingmanson 1996; Hohmann and Fruth 2003a). To compare bonobos and chimpanzees, I relied on the tool use catalogue compiled by Beck (Beck 1980) because it represented at the time of the study the most up-to-date published catalogue for captive chimpanzees. To facilitate comparison between the chimpanzee and bonobo catalogues, I introduced a few minor modifications in terminology and classifications. I included all contexts and behaviours described by Beck's original list to enable the broadest possible comparison between the two species and sorted the collected data accordingly (Table 3.1; see Appendix B for definitions, descriptions, and page numbers used by Beck 1980). I also introduced a new context to describe observations collected in the bonobo populations ('Sex', see results). As it was not possible to compare frequency data in a systematic way (because some of the published records did not provide them), I considered any report or observation of distinct tool behaviour in captive bonobos or wild chimpanzees as an indication that the tool behaviour was present in this population.

**Inter-observer reliability test**

Data collection started after Z.C. and I were able to identify individuals without difficulties. In case of doubts, experienced field assistants were always present and could be consulted to confirm identity. I conducted an inter-observer reliability test in which Z.C. and I independently coded 21 video clips containing tool use behaviours of bonobos at Lola ya Bonobo. The featured tool behaviours represented 18.5% of the entire tool catalogue recorded at Lola performed by 10 different individuals (group 1: N = 8; group 2: N = 2). Reliability in tool classification and recognition of individuals was perfect at 100% with no disagreements or omissions.

**Data analyses and statistics**

I used the tool use catalogues to determine whether there were systematic differences in tool use behaviour both between the two species (chimpanzee vs. bonobo) and between habitat types (wild vs. captivity). For this analysis, I determined whether or not a tool behaviour (i.e., each line in Table 3.1) was present in the four groups (e.g., wild chimpanzees). To enable systematic comparisons, I removed all tool behaviours that could not have occurred naturally (e.g., if they were part of a specific experiment). I then conducted Pearson Chi-Square tests to compare the diversity of tool-using behaviours in each of the four groups (wild chimpanzees, wild bonobos, captive chimpanzees, captive bonobos) and to determine if species membership or habitat type had significant effects on the observed proportion relative to all possible tool behaviours. In a second analysis, I compared the two species in captivity per context. This way I could rule out that the effects were due to unequal contributions by some contexts in terms of the number of observed tool behaviours. I could not carry out this analysis with wild populations since the bonobo tool set was too small to analyse statistically.

To investigate whether there were systematic sex and age differences in bonobo tool use, I analysed data collected at Lola ya Bonobo as time of observation was counter-balanced between individuals, ensuring that tool use differences did not result from an observational bias. Using Univariate Analyses of Variance, I compared individuals in terms of their contributions to the catalogue both for tool behaviours and tool-related behaviours (e.g., using a hard surface to crack a fruit). For each individual, I entered sex (male vs. female) and age class (adult vs. non-adult) as fixed factors and tool variety (the total number of different

tool behaviours produced by the individual) as the dependent variable. I excluded one female (MM) from these analyses because she was human-raised before coming to the sanctuary at the age of 18. I first determined the general effect of sex and age class on the total number of observed tool behaviours, and then conducted the same analysis per context. All statistical tests were two-tailed and conducted with SPSS v 17.0 (copyright © SPSS Inc.).

## 3. Results

### Species differences

Following Beck (1980), I discriminated 63 different tool behaviours in 14 contexts, each containing 1 to 9 actions (mean = 2.7, SD = 2.4; Table 3.1). Direct comparisons between chimpanzees and bonobos, both in the wild and in captivity, were possible over 52 behaviours. I excluded 11 tool behaviours because they involved contexts that were not available to captive individuals, did not occur during the time of the study (e.g., hunting, rainstorms) or because they were not spontaneous but artificially elicited as part of other ongoing behavioural experiments (see italic fields, Table 3.1).

I first compared the four datasets in terms of overall differences in tool use in the four groups (wild chimpanzees, captive chimpanzees, wild bonobos, captive bonobos). Of the 52 tool behaviours, captive chimpanzees produced 47, wild chimpanzees 44, captive bonobos 42 and wild bonobos 8. Comparisons revealed an overall effect of species ($\chi^2_1 = 37.01$, $p < 0.001$) and habitat ($\chi^2_1 = 30.14$, $p < 0.001$). However, when analysing the tool use behaviour of the two species separately, I found no differences between wild and captive chimpanzees ($\chi^2_1 = 0.79$, $p = 0.37$), but a significant difference between captive and wild bonobos ($\chi^2_1 = 44.53$, $p < 0.001$). When analysing the two habitat types separately, I found no difference between captive chimpanzees and bonobos ($\chi^2_1 = 1.95$, $p = 0.16$) but a significant difference between wild chimpanzees and bonobos ($\chi^2_1 = 49.85$, $p < 0.001$). Thus, the differences reported in the previous analysis resulted from the contribution of the wild bonobos only: of all 52 tool behaviours, only eight have so far been reported from wild bonobos (compared to 44 in wild chimpanzees). Of all 52 tool behaviours, only seven were different in captive bonobos and chimpanzees. Of these seven, one (dental auto-grooming) was not found in captive bonobos, although it has been observed in the wild.

**Table 3.1.** Summary of tool-using behaviours in wild and captive chimpanzees and bonobos.

| | | | | Chimpanzee | | Bonobo | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Context** | **#** | **Action** | **Behaviour** | **Wild** | **Capt** | **Savage, 1976** | **Jordan, 1982** | **Gold, 2002** | **Ingm., 1996** | **Lola ya Bonobo** | **Note** | **Capt** | **Comp** |
| **Antagonism** | 1 | Brandishing tools | Agonistic intimidation displays | Yes | Yes | | Yes | | | Yes | | Yes | ✔ |
| | | | Immature Agonistic intimidation displays | Yes | Yes^ | | | | | No | | No | ✘ |
| | | | Sticks in rain storm | Yes | Yes | | | | | ? | No rain storm witnessed | ? | n/a |
| | | | Wave tools against flies | Yes | No | | | | Yes | No | In the wild | No | ✔ |
| | | | Sticks in play | Yes | Yes | | Yes | | Yes | No | Twycross and San Diego | Yes | ✔ |
| | 2 | Dragging tools | Dragging, rolling, and/or kicking objects during display (conspecific) | Yes | Yes | | Yes | Yes% | Yes | Yes | Twycross and San Diego | Yes | ✔ |
| | | | Dragging, rolling, and/or kicking objects during display (heterospecific) | Yes | Yes^ | | | | | No | Twycross and San Diego | Yes | ✔ |
| | | | Dragging branches during rainstorm | Yes | Yes | | | | | ? | No rainstorm witnessed | ? | n/a |
| | | | Dragging during social play | Yes | Yes* | | Yes | | | Yes | Twycross | Yes | ✔ |
| | 3 | Unaimed throwing | Unaimed throwing in arousal states | Yes | Yes | Yes | | | | Yes | Twycross | Yes | ✔ |
| | | | Unaimed throwing in reaction to other species | Yes | Yes^ | | | | | Yes | | Yes | ✔ |
| | | | Unaimed throwing during social interaction | Yes** | Yes | | Yes | | | No | Twycross and San Diego | Yes | ✔ |
| | | | Unaimed throwing resulting from frustration | Yes** | Yes | | | | | Yes | Twycross | Yes | ✔ |
| | | | Unaimed throwing during play | Yes | Yes^ | | Yes | | | Yes | Twycross | Yes | ✔ |
| | 4 | Aimed throwing | Aimed throwing during agonistic interaction | Yes | Yes | Yes | Yes | | | Yes | | Yes | ✔ |
| | | | Interspecific aimed throwing | Yes | Yes | | Yes | | | Yes | | Yes | ✔ |

| (continued) | | | | Chimpanzee | | Bonobo | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Context** | **#** | **Action** | **Behaviour** | **Wild** | **Capt** | **Savage, 1976** | **Jordan, 1982** | **Gold, 2002** | **Ingm., 1996** | **Lola ya Bonobo** | **Note** | **Capt** | **Comp** |
| **Antagonism** (continued) | 4 | Aimed throwing (continued) | Interspecific aimed throwing (Hunting) | Yes | *X* | | | | | *X* | | *X* | n/a |
| | | | Aimed throwing during social play | Yes** | Yes | | Yes | | | Yes | Twycross | Yes | ✔ |
| | 5 | Dropping | Interspecific dropping | Yes | Yes | | | | | No | San Diego | Yes | ✔ |
| | | | Conspecific dropping during social play | Yes | No | | | | | No | | No | ✔ |
| | | | Conspecific dropping during agonistic episodes | Yes | Yes | | | | | No | | No | ✘ |
| | 6 | Clubbing | Interspecific clubbing | Yes | Yes | | Yes | Yes | | No | | Yes | ✔ |
| | | | Social play conspecific clubbing | Yes | Yes | | | | | Yes | Twycross | Yes | ✔ |
| | 7 | Prodding or jabbing | Conspecific prodding or jabbing during agonistic contexts | Yes** | Yes | | Yes | | | Yes | Twycross | Yes | ✔ |
| | | | Interspecific prodding or jabbing | Yes** | Yes | | | | | Yes | | Yes | ✔ |
| | | | Insect or animal spearing | Yes¤ | Yes | | | | | No | | No | ✘ |
| | 8 | Tree pounding | Pound on tree buttresses (or equivalent) during agonistic displays | Yes | Yes^ | | | | | Yes | Twycross and San Diego | Yes | ✔ |
| | 9 | Frustration pounding | Pound on objects after unsucessful attempts | *X*# | Yes | | | | | ? | | ? | n/a |
| **Grooming** | 1 | Dental grooming | Dental Allogrooming | No | Yes | | | | | No | | No | ✘ |
| | | | Dental Autogrooming | Yes | Yes*** | | | | Yes | No | In the wild | No | ✘ |
| | 2 | Grooming | Interspecific Grooming | No | Yes | | | | | Yes | On dogs and humans | yes | ✔ |
| | | | Self-Grooming using tools | Yes*** | Yes | | | | Yes | Yes | | yes | ✔ |
| **Escape** | 1 | Escape enclosure | Use of sticks as pitons to escape enclosure | *X* | Yes | | | | | ? | No attempt of escape witnessed | ? | n/a |

| (continued) | | | | Chimpanzee | | Bonobo | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Context** | **#** | **Action** | **Behaviour** | **Wild** | **Capt** | **Savage, 1976** | **Jordan, 1982** | **Gold, 2002** | **Ingm., 1996** | **Lola ya Bonobo** | **Note** | **Capt** | **Comp** |
| **Play** | 1 | Infant Termite fishing | Insert and Probe in termite mounds (or equivalent) | Yes | Yes | | | | | Yes | Twycross and San Diego | Yes | ✔ |
| | 2 | Playful pounding | Pound objects on others for playful purpose | Yes^ | Yes | | | | | Yes | Twycross | Yes | ✔ |
| | 3 | Playful exploration | Exploration with stick | Yes** | Yes | | | | | Yes | | Yes | ✔ |
| **Oddness / Inaccessibility** | 1 | Using tool if reluctant to touch with hand or if object of interest inaccessible | Touching inhabitual objects | Yes | Yes | | Yes | | | ? | | Yes | ✔ |
| | | | Interspecific Touching | Yes** | Yes | | | | | Yes | San Diego | Yes | ✔ |
| **Balancing and climbing** | 1 | Secure object | Secure object (e.g.: suspended food) | *No* | Yes | | Yes | | | ? | | Yes | ✔ |
| | 2 | Playful balancing | Playful balancing | No | Yes | | | | | Yes | Twycross | Yes | ✔ |
| **Propping and climbing** | 1 | Secure suspended food | Secure suspended food | *No* | Yes | | | Yes | | ? | | Yes | ✔ |
| | 2 | Escape enclosure propping | Escape enclosure propping | *X* | Yes | | Yes | | | ? | | Yes | ✔ |
| **Stacking** | 1 | Access to suspended lures or extended vision | Gain access to suspended lures or to extended vision | *No* | Yes | | Yes | | | ? | | Yes | ✔ |
| | 2 | Escape enclosure stacking | Escape enclosure stacking | *X* | Yes | | | | | ? | No attempt of escape witnessed | ? | n/a |
| **Food acquisition** | 1 | Termite fishing | Insert and Probe in mounds or nests of termites | Yes | Yes | | Yes | | | X | Twycross and San Diego | Yes | ✔ |
| | | | Perforate termite mound | Yes | *X* | | | | | *X* | No termite mound in captivity | *X* | n/a |
| | 2 | Ant Dipping | Dipping for fossorial ants | Yes | Yes | | | | | ? + | No ant trail seen in zoos | ? | n/a |
| | | | Dipping for arboreal ants | Yes | No | | | | | ? + | No ant trail seen in zoos | ? | n/a |
| | 3 | Honey or other food fishing | Insert tool and probe in bee/artificial nest | Yes | Yes | | | | | X | Twycross and San Diego | Yes | ✔ |
| | 4 | Reaching food or object | Reaching and retrieving food lures or objects | *No* | Yes | | Yes | | | Yes | Twycross | Yes | ✔ |

| (continued) | | | | Chimpanzee | | Bonobo | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Context** | **#** | **Action** | **Behaviour** | **Wild** | **Capt** | **Savage, 1976** | **Jordan, 1982** | **Gold, 2002** | **Ingm., 1996** | **Lola ya Bonobo** | **Note** | **Capt** | **Comp** |
| **Food acquisition (continued)** | 5 | Opening tough rinds or shells | Nut cracking | Yes | Yes | | | | | Yes | | Yes | ✔ |
| | | | Hard-shell fruit cracking | Yes | No | | | | | Yes | | Yes | ✘ |
| | 6 | Enlargement of openings | Nest opening | Yes | Yes | | Yes | | | ? | | Yes | ✔ |
| | 7 | Ant wiping | Ant wiping | Yes | No | | | | | No | | No | ✔ |
| **Digging** | 1 | Digging | Digging | Yes | Yes | | | | | Yes | Never eat what is dug | Yes | ✔ |
| **Cleaning** | 1 | Cleaning body | Cleaning body, wound or menses | Yes | Yes | | Yes | | Yes | Yes | | Yes | ✔ |
| | 2 | Cleaning surface | Cleaning outer space | *X* | Yes | | Yes | | | Yes | Twycross | Yes | ✔ |
| **Liquids** | 1 | Water sucking | Insert tool into concavities or plain water and suck water from it | Yes | Yes | | Yes | | | No | | Yes | ✔ |
| | 2 | Leaf-sponging | Leaf-sponging | Yes | Yes | | | | | No | In the wild § and Twycross | Yes | ✔ |
| | 3 | Fluids absorbing | Fluids absorbing | Yes | No | | | | | No | | No | ✔ |
| | 4 | Containers | Fluid container | Yes | Yes | Yes | Yes | | | Yes | Twycross and San Diego | Yes | ✔ |
| **Baiting** | 1 | Baiting | Using any kind of object to bait animals to lure them within reach | No | Yes | | | | | No | | No | ✘ |
| **Draping** | 1 | Draping | Draping objects on one's body | Yes | Yes | | | | Yes | No | Twycross and San Diego | Yes | ✔ |

Data for chimpanzees were from Beck (1980) and other sources (see references). Minor modifications in terminology and classifications were necessary to facilitate comparisons. Data for bonobos were taken from published studies (see references) and complemented by my own data. General contexts were divided into different functional categories ('Action'), which could be further divided into tool use variants ('Behaviour'). The next two columns describe if wild chimpanzees and captive chimpanzees have been observed with the behaviour. The next columns describe if the behaviour has been observed in different captive and wild bonobo studies (see text for description). Finally the column Lola ya Bonobo sums up the observations recorded at Lola ya Bonobo sanctuary. The summary of the captive studies is given in the Captivity column. Finally a comparison between chimpanzees and bonobos in captivity is given in the last column: when the behaviour is similarly present or absent in the captive populations of the two species, the panel receives a tick; otherwise it receives a cross. Yes: behaviour present. No: behaviour not present. ?: presence of the behaviour unknown. n/a: comparison non applicable. *X* panel: settings non applicable for wild (experimental setting) or captive (hunting) animals. *No* panel: behaviours absent in the wild, maybe because of a lack of need to develop it. X: behaviours not observed because of experimental settings or natural artefacts not found in captivity. +: behaviour not observed within observation range in cleared areas but no control of the forest areas. %: quoting (Walraven et al. 1993). * e.g.: (Jensvold and Fouts 1993). ** (van Lawick-Goodall 1968). *** (Goodall 1986). ¤ (Pruetz and Bertolani 2007). #: pounding exists during food acquisition (Yamakoshi and Sugiyama 1995). §: (Hohmann and Fruth 2003a). ^: personal observations. Ingm., 1996: Ingmanson, 1996.

Subsequently, I conducted a context analysis and found that the tool use catalogues of captive bonobos and chimpanzees were identical for nine of 13 possible contexts ('Play', 'Oddness', 'Balancing', 'Propping', 'Stacking', 'Digging', 'Cleaning', 'Liquids', 'Draping'; 'Escape' was not included as no attempt was ever witnessed). In other words, all the behaviours observed in captive chimpanzees had also been observed in at least one of the captive bonobo groups. Additionally, I found no significant differences in two other contexts ('Antagonism', $\chi^2_1 = 1.51$, $p = 0.22$; 'Food acquisition': $\chi^2_1 = 0.42$, $p = 0.52$). Tool use was also observed in both captive chimpanzees and bonobos during 'Grooming', but only wild bonobos used tools during dental grooming. The only context that differed between chimpanzees and bonobos was 'Baiting' with no observations in wild or captive bonobos.

**Sex differences**

I compared tool-related behaviours of 17 bonobos at Lola (8 females; 9 males; Table 3.2). Following Beck (1980), I was able to compare the effects of age and sex class for 27 behaviours in 7 contexts. The most represented contexts at Lola were 'Play' and 'Food acquisition' with respectively 9 and 7 different behaviours observed. There was no significant difference in the average number of tool or tool-related behaviours between adult (mean of 8.12, SD = 1.30) and non-adult individuals (mean 5.89, SD = 1.15; ANOVA, $F_{1,15} = 0.43$, $p = 0.52$, Fig. 3.1a). However, there was a significant sex effect with females showing a larger average number of behaviours (mean of 9.37, SD = 1.33) than males (mean of 4.78, SD = 0.55; ANOVA, $F_{1,15} = 8.15$, $p = 0.014$, Fig. 3.1b). I found no interaction between the two factors (ANOVA, $F_{1,15} = 0.19$, $p = 0.67$).

**Table 3.2.** Summary of the tool use observed at Lola ya Bonobo.

| | **Action** | **Behaviour** | AF | | | | | | SF | | | AM | | | SM | | | JM | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | MM | SW | OP | BD | KL | SL | NO | IS | LK | TT | MN | KW | MA | BN | MI | KG | IB | KD |
| **Antagonism** | Agonistic intimidation displays | Agonistic intimidation displays using branch (natural) | 1 | 1 | 1 | | 1 | | | 1 | | 1 | 1 | 1 | 1 | 1 | | 1 | | |
| | Agonistic intimidation displays | Agonistic intimidation displays using bottle (artificial) | 1 | 1 | 1 | | 1 | | | | | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 |
| **Play** | Playful pounding | Mud bashing with stick | | | | 1 | | | | | 1 | | | | | | | | | |
| | | Conspecific beating | | | | | | | 1 | | | | | | | | | | | |
| | | Interspecific poking | | | | | | | 1 | | | | | | | | | | | |
| | Playful balancing | Bottle balancing | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | | | 1 | 1 | 1 |
| | Pretend play | Fake drinking | | 1 | 1 | | | 1 | 1 | 1 | | | | | | | | 1 | | |
| | | *Pretend milk feeding through fence* | | | | | | | 1 | | | | | | | | | | | |
| | Playful containers | Bottle filling to play | | 1 | | 1 | | | | | | 1 | | | | | | 1 | | |
| | | *Pouring water in bottle submerged in lake* | | 1 | | | | | | | | | | | | | | | | |
| | Playful rolling | *Using fruit (coconut) as play tool* | | | | | | | 1 | | | | | | | | | | | |
| **Food acquisition** | Opening tough rinds or shells | Nut cracking with stone hammer and anvil | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | | 1 |
| | | Nut cracking using concrete as an anvil | | | 1 | 1 | 1 | | 1 | | 1 | | | | | | 1 | | | |
| | Opening tough rinds or shells | Forest fruit cracking using stone anvil | | 1 | 1 | 1 | | | 1 | | | | | 1 | | | | | 1 | 1 |
| | | Forest fruit cracking using branch anvil | | | | | | | | | | | | 1 | | | | | | |
| | | Forest fruit cracking using palm trunk | | 1 | | | 1 | | 1 | | | | | | | | | | | 1 |
| | | Forest fruit cracking using another fruit | | 1 | 1 | 1 | 1 | 1 | | | 1 | | | | | | 1 | | | |
| | Reaching food or object | Raking objects out of the enclosure | | | 1 | | | | 1 | | | | | | | | | | | |
| **Digging** | Digging | Digging with stick | | 1 | | 1 | | 1 | 1 | | | 1 | | | | | | | | |

| (continued) | **Action** | **Behaviour** | AF | | | | | | | | | AM | | | SM | | | JM | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | MM | SW | OP | BD | KL | SL | NO | IS | LK | TT | MN | KW | MA | BN | MI | KG | IB | KD |
| **Cleaning** | Cleaning body | *Using leaves to clean body* | | | | | | | | | | | 1 | | | | | | | |
| | Cleaning surface | *Sweep using palm* | | 1 | | | | | | | | | | | | | | | | |
| **Liquids** | Containers | Bottle filling | | 1 | | | | 1 | | 1 | | | | | | | | 1 | | |
| | | Using human-made objects as recipients to drink | | 1 | | | | 1 | 1 | | | | | | | | | | | |
| | | Using fruit shell as a recipient to drink | | 1 | | | 1 | 1 | | | | | 1 | | | | | 1 | | 1 |
| | | *Bottle pouring into another bottle or into lid* | | 1 | | | | | | | | | | | | | | | | |
| **Sex** | Sexual stimulation | Genital stimulation using human-made object | | | | | | 1 | | 1 | | | | | | | | 1 | 1 | |
| | | *Using fruit (coconut) as sexual stimulator* | | | | | | | 1 | | | | | | | | | | | |
| **Total** | | | **2** | **16** | **9** | **8** | **8** | **9** | **14** | **6** | **5** | **4** | **5** | **6** | **4** | **3** | **4** | **8** | **3** | **6** |

See Table 3.1 for terminology and Appendix C for the complete information about the bonobos at Lola. '1' indicates that the behaviour has been observed. AF: adult females. SF: sub-adult females. AM: adult males. SM: sub-adult males. JM: juvenile males. *Italic*: Idiosyncratic behaviours. Infants were excluded from the analysis.

At the context level, I was able to compare 'Antagonism', 'Play', 'Food acquisition' and 'Liquids'. 'Digging' was absent in males but present in females. The sample size for 'Cleaning' was too small to allow statistical analysis as it was observed once in a male and once in a female. I found no effect of age class on any of the contexts (ANOVA, 'Antagonism': $F_{1,15} = 4.04$, $p = 0.057$; 'Play': $F_{1,15} = 0.50$, $p = 0.49$; 'Food acquisition': $F_{1,15} = 0.009$, $p = 0.93$; 'Liquids': $F_{1,15} = 0.29$, $p = 0.60$). Similarly, I found no sex effects for 'Antagonism' and 'Liquids' (ANOVA, 'Antagonism': $F_{1,15} = 4.04$, $p = 0.066$; 'Liquids': $F_{1,15} = 1.36$, $p = 0.26$), but significant effects for play and food (ANOVA, 'Play': $F_{1,15} = 8.91$, $p = 0.011$; 'Food acquisition': $F_{1,15} = 8.02$, $p = 0.014$) due to females having a larger diversity of tool-using behaviours than males (females: 'Play': 3.00 ± 1.58; 'Food acquisition': 4.00 ± 1.41; males: 'Play': 1.00 ± 0.87; 'Food acquisition': 1.00 ± 1.24, means ± SD). No significant interactions were found between the main factors in any context (ANOVA, 'Antagonism': $F_{1,15} = 0.002$, $p = 0.97$; 'Play': $F_{1,15} = 0.50$, $p = 0.49$; 'Food acquisition': $F_{1,15} = 1.12$, $p = 0.31$; 'Liquids': $F_{1,15} = 0.73$, $p = 0.41$).

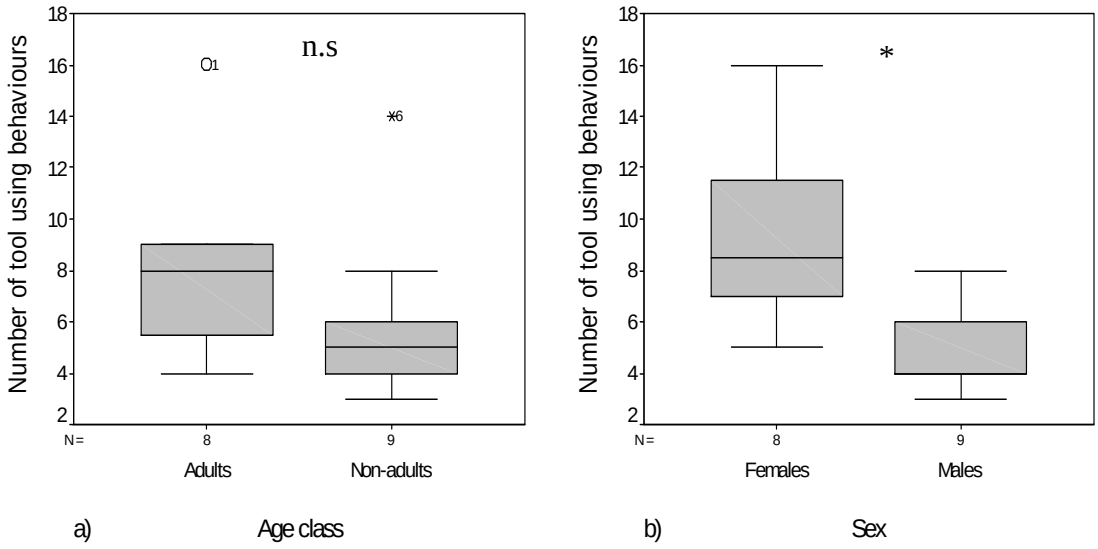


**Figure 3.1.** Box plots presenting the number of tool-using behaviours observed at Lola by age and sex. The dark line in the middle of the plots is the median of the number of tool-using behaviours for each age or sex class. *: $p < 0.05$; n.s.: non-significant.

**Specific behaviours (Lola ya Bonobo)**

The bonobos at Lola used tools in seven general contexts. 'Play' and 'Food acquisition' were the most common ones in which tool use occurred, with nine and seven different types, respectively. I added 'Sex' as an additional context to Beck's (1980) classification, which contained two behaviours: using natural material (e.g., fruits) or artefacts (e.g., bottles) for sexual stimulation. Tool use in a sexual context was also observed in San Diego and Twycross (Z.C., personal observation). I also observed a number of seemingly idiosyncratic behaviours in the 'Play', 'Cleaning', 'Liquids' and 'Sex' contexts (Table 3.2). In the following, I describe some of these observations in more detail, because they have implications for the underlying cognitive capacities.

*'Pretend' milk feeding*

At noon, caretakers feed the bonobos soymilk through the fence using plastic bottles. The individuals usually keep the bottles and some continue to play with them, for instance by taking them over to the nearby lake to repeatedly fill them and pour out their contents. On one occasion, a sub-adult female, Nioki, filled her bottle in the lake, but then brought it back to the fence where she had previously been fed by a caregiver. She then passed the bottle and her arm through the fence, aimed the bottle at herself and started pouring water into her mouth. She did not seem to ingest any of the water, but instead adopted her typical facial expression while being fed by a caretaker, as if pretending to drink soymilk (Fig. 3.2).

*Using fruit shells as containers*

A number of times, bonobos were observed using shells of fruits (such as *Strychnos*) as containers for water or soymilk. One adult female, Semendwa, was frequently observed pouring liquid between the shells, bottles, and lids. This behaviour had no apparent function, and I therefore assigned it to the 'Play' context, although she sometimes used this technique to share milk with her daughter.

**Figure 3.2.** 'Pretend' soymilk drinking by a sub-adult female (Nioki) at Lola ya Bonobo. Half an hour after the end of the 'soymilk feeding', the female carried an empty bottle, used previously by the caretaker, to the nearby lake, filled it with water, and then brought it back to the fence. She then passed the bottle through the fence and poured water into her mouth without ingesting any, while adopting the 'milk-feeding' facial expression, as if pretending to drink soymilk (drawing: Jason Zampol).

## 4. Discussion

### Chimpanzee and bonobo tool use

The tool use behaviour of non-human primates is relevant for theories of human evolution (Washburn 1960; Parker and Gibson 1979) and the natural tool use behaviour of our closest living relatives, the chimpanzees and bonobos, play a key role in this comparison. However, no systematic comparison had been conducted so far. Previous research has shown that, in terms of cognitive and physical abilities to use tools, bonobos and chimpanzees do not differ in relevant ways (Takeshita and Walraven 1996; Herrmann et al. 2008). My study is in line with these results by demonstrating that, in captivity, bonobos and chimpanzees do not differ in their overall diversity of tool-using behaviours. Bonobos showed a large portfolio of tool-using behaviours that did not differ from chimpanzees either in quantitative or qualitative terms. This conclusion is based on published studies and the current analysis of data from four captive facilities. Out of 52 tool behaviours, only seven were different between captive bonobos and chimpanzees. One of them (dental auto-grooming) has been observed in wild bonobos, suggesting that it is part of the species' behavioural repertoire. All contexts in which chimpanzees used tools were also found in bonobos, with only one exception ('Baiting', which consists in attracting another living-being within reach with a tool).

The general diversity of tool-using behaviours was comparable in the two species, although some differences remained in terms of context-specificity and functional use. Wild chimpanzees predominantly use tools in the context of food acquisition (McGrew 1979; Boesch and Boesch 1990) while wild bonobos appear to use tools mainly for personal care (cleaning, protection from rain) and social purposes (Ingmanson 1996). My observations at Lola ya Bonobo are in line with these observations, i.e. that tool use is not just used to acquire food. Instead, I found the largest diversity of tool-using behaviours in the 'Play' context. Another difference was in the use of tools for sexual stimulation, something that has been reported for orangutans but not chimpanzees (van Schaik et al. 2003). As my study could not compare the frequency of the different tool use behaviours, it is possible that some more subtle species differences are also present in terms of usage.

**Tool use in bonobos reflect their juvenile, not their social characteristics**

Observations in the wild and in captivity have led to the hypothesis that bonobo tool use has mainly a social function (de Waal 1986; Ingmanson 1996). However, my own observations are not entirely consistent with this interpretation despite the fact that a considerable proportion of tool use was observed in the play context. Most play-related tool use in bonobos was part of solitary, not social, play. Although social games with objects have been observed in bonobos interacting with humans (Pika and Zuberbühler 2008), I did not record any shared tool use *between* bonobos in this context. Even if sometimes two or more bonobos simultaneously played with bottles, these activities remained solitary. One possible exception was a sub-adult female (Nioki), whom I observed using a stick to playfully beat an infant, while both produced laughter, an indicator of friendly motivations (Davila Ross et al. 2009). However, I did not see any exchange of gaze between the two individuals, suggesting that the behaviour did not serve a joint social purpose (Tomasello et al. 2005). I frequently observed playful stick beating in solitary bonobos and this was often accompanied by a characteristic 'play face' (Palagi 2008). In the wild, solitary play is also common in bonobo infants, while social play is comparably rare (Ingmanson 1996).

Perhaps the most striking difference that emerged from this report is the observation that, at Lola ya Bonobo, nearly all fully-grown individuals engaged in tool-based play behaviour, such as 'bottle filling', regardless of their age or social position. While young chimpanzees spend much time playing, this is not so much the case for the adults, especially the males (de Waal 1982; Goodall 1986). It has been argued that bonobos have been subjected to an evolutionary pressure towards neoteny, in that they have retained some juvenile characteristics in adulthood (Shea 1983; Wrangham and Pilbeam 2001; Wobber et al. 2010), a hypothesis also supported by my observations. High levels of play are common in adult bonobos (Palagi 2006; Palagi and Paoli 2007) and this study shows that tools are an integral part of this behaviour. In chimpanzees, however, adult play is very rarely observed (Pellis and Iwaniuk 2000). If adult play is observed in wild groups, it does not appear to involve the use of tools, in contrast to infant and juvenile play, which often involves twigs, branches and leaves (personal observations).

**Female bias in tool use in the *Pan* genus**

Another key finding of my study is the sex differences in bonobo tool use behaviour. Similar to chimpanzees (McGrew 1979; Boesch and Boesch 1990), I found that bonobo females were more avid tool-users compared to males, and that they were using a larger diversity of tools. At Lola ya Bonobo, females displayed a larger range of tools or tool-related behaviours during food acquisition and play than males, although both sexes used tools in all contexts apart from one. Only females used sticks to dig in the mud. To date, no such bias has been found in wild orang-utans (Fox et al. 2004; van Schaik, personal communication), the only other skilful ape tool-users in the wild. Data on gorillas, whether in the wild (Breuer et al. 2005; Wittiger and Sunderland-Groves 2007) or in captivity (reviewed in Lonsdorf et al. 2009), are too limited to draw conclusions. Apart from apes, a female bias in tool use has also been found in dolphins (Mann and Sargeant 2003). One explanation for the female bias is that mothers and daughters tend to remain close until late adolescence in both chimpanzees (Lonsdorf et al. 2004) and dolphins (Mann 2009), while sons become independent earlier and are thus less exposed to their mother's skills.

In wild chimpanzees, the acquisition of tool use behaviour in infants appears to be partly socially learned from the mother or other experienced individuals (Matsuzawa et al. 2001; Lonsdorf 2005), suggesting that similar processes may be at work in bonobos. At Lola ya Bonobo, bonobos typically arrive as orphans at a very young age, suggesting that they have had only very limited previous exposure to their biological mother and any of her acquired skills. Newly arriving infants are first looked after by humans, before integration into one of the groups where they are sometimes cared for by an existing group member. During this process, male and female infants are equally exposed to various tool use behaviours of their human and conspecific caretakers, indicating that the observed sex bias in bonobo tool use behaviour cannot be explained with differences in rearing conditions. More likely, female infant bonobos are more receptive to tool-using models, more motivated to interact with artefacts, or they are simply more patient. I also found that female bonobos employed a larger number of techniques to solve one particular problem than males (e.g., opening a hard-shelled fruit), suggesting that they were better able to dissociate means from their ends.

One can only speculate about the functional significance of the observed sex difference in the *Pan* genus. Perhaps females have evolved more sophisticated tool skills due to the higher nutritional demands of pregnancy and infant care. Whether female-biased tool use was shared

with a common ancestor with modern humans is equally speculative. Finally, this finding should be complemented with ecologically valid observations in the wild, ideally from different groups facing different ecological constraints (McGrew 1989).

**Flexibility in bonobo tool use and genetic predispositions for culture**

Flexibility is a key characteristic of higher cognitive capacities, something that has been repeatedly demonstrated in chimpanzees (Bruner 1972; Tomasello and Call 1997). I found a number of seemingly idiosyncratic behaviours by some individuals at Lola, some of which intriguingly complex. An interesting example was the use of fruit shells or skins as containers. These items were not treated as fruits, but as items with specific functional properties as tools (e.g.: pepper, Jordan 1982). Another example concerned the sequential use of two tools, as part of the daily routine for the female Semendwa during which she used lids (*Strychnos* shells) or plastic bottles to transfer water between the different containers. Finally, Nioki's 'pretend soymilk feeding', seen by two observers (T.G., Z.C.), is equally noteworthy and could be a case of pretence play. Although I cannot rule out that Nioki, as well as other individuals who engaged in similar behaviour, did not ingest some of the water, most was pouring out of their mouths and they often adopted a play-face during the act, raising doubts that they were interested in the functional aspect of the behaviour. Secondly, in Nioki's case, she first passed her arm with the container through the fence, hereby reproducing the movement patterns of the daily soymilk feeding events (see Fig. 3.2). Had she just been interested in drinking, these actions could not be explained. Studies that focus on the cognitive abilities underlying tool use are equally relevant. In one of them, gorillas performed as well as bonobos, but both species did not appear to understand the causality of the task while a chimpanzee and two orangutans appeared to do so (Mulcahy and Call 2006b). Although this finding matches with the current dichotomy in ape tool use in the wild, there are other studies that found no cognitive differences or limitations in other aspects of tool use. For example, both gorillas and orang-utans are able to represent relevant aspects of experimental tool tasks (Mulcahy et al. 2005) while both bonobos and orangutans are able to plan ahead by saving tools for a specific future use (Mulcahy and Call 2006a). Finally, there does not seem to be a profound difference amongst great apes in their ability to represent the functional properties of tools (Herrmann et al. 2008).

These observations illustrate that bonobos are no different from chimpanzees in terms of the flexibility associated with the behaviour, especially in the play context (Jensvold and Fouts 1993). In line with the recent experimental studies (Mulcahy and Call 2006a; Herrmann et al. 2008), my observations support the hypothesis that the cognitive mechanisms responsible for this flexibility are shared by both species and have most likely evolved prior to their split about one million years ago (Won and Hey 2005). Similarly to rooks (chapter 1; Tebbich et al. 2007), the bonobo is one of many species which profit from an evolutionary ancient trait selected at a certain point because of its adaptiveness but no longer adaptive in the current habitat where the species are found nowadays (see chapter 7). Given that the two species of the *Pan* genus share a similar propensity to use tools, and that the same female bias is found, it is likely that these two characteristics were already present in their common ancestor. In other words, the cognitive prerequisites for bonobos to develop a 'chimpanzee-like' culture are all present, but for unknown reasons, it does not develop in their natural habitat. In my analysis, wild bonobos differed considerably from captive groups and from chimpanzees in captivity and the wild. Two main lines of explanation can be proposed. First, it is possible that tool use in wild bonobos has simply been underestimated because long-term observations are absent and because the number of studied groups is still small (Hohmann and Fruth 2003a). Second, bonobos may have lost tool use in the wild, not because they are cognitively incapable but because all relevant food sources can be accessed without the help of artefacts (McGrew et al. 1997: hypothesis 8; Hohmann and Fruth 2003a). Although chimpanzees are capable tool-users, some groups, such as the Sonso community, have very small repertoires but live concurrently in a rich environment (Reynold 2005). This hypothesis may thus also be proposed to explain their limited tool use (see chapters 6 and 7).

Before firm conclusions can be made, more data on bonobo and gorilla tool use are needed beyond the existing records (bonobos: Kano 1982; Ingmanson 1996; Hohmann & Fruth 2003; gorillas: Breuer et al. 2005; Wittiger & Sunderland-Groves 2007). Overall, the data are more compatible with the hypothesis that both gorillas and bonobos are able to develop a large portfolio of tool use in the wild, but that the environment prevents this development. Comparing the impact of habitat differences on the development of tool use in all apes is likely to provide progress, as are data on populations that spend much time on the ground or forage in open savanna-type habitats (e.g. Myers-Thompson 2002). Habitat type and use, in other words, are likely to play a key causal role in the emergence and maintenance of tool use in wild ape populations (see chapter 6).

# Chapter four: Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task

Results from this study have been published in:

**Gruber, T.**, Muller, M.N., Strimling, P., Wrangham, R.W. & Zuberbühler, K. (2009) Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. Current Biology, 19(21): 1806-1810.

## Summary

Population and group-specific behavioural differences have been taken as evidence for animal cultures, a notion that remains controversial with sceptics arguing that ecological or genetic factors, rather than social learning, provide a more parsimonious explanation. Work with captive chimpanzees has addressed this criticism by showing that experimentally created traditions can be transmitted through socially-aided learning. Recent fieldwork further suggests that ecological and genetic factors are insufficient to explain all the behavioural differences seen in chimpanzees, but the data are only observational. In this chapter, I present the results of a field experiment that compared the performance of chimpanzees from two Ugandan communities, Kanyawara and Sonso, on an identical task in the physical domain: extracting honey from standardised holes drilled into horizontal logs. Kanyawara chimpanzees, who occasionally use sticks to acquire natural honey, spontaneously manufactured sticks to extract the experimentally provided honey. In contrast, Sonso chimpanzees, who possess a considerable leaf technology but no food-related stick use, relied on their fingers, but some individuals also produced leaf-sponges to access the honey. My results thus indicate that chimpanzees rely heavily on what they know when encountering a new feature in their environment, and that they do not experiment with new solutions on a trial-and-error basis. Additionally, no chimpanzee at Sonso ever used a stick, and no chimpanzee in Kanyawara ever used a sponge, suggesting that this segregation of means to attain the same goal could be cultural. These data show that an experimental investigation of culture in several populations of chimpanzees is possible in the wild through the use of simple cognitive tests and that, when genetic and environmental factors are controlled for, wild chimpanzees rely on their cultural knowledge to deal with a novel task.

## 1. Introduction

Some of the strongest evidence for animal culture comes from studies on wild chimpanzees comparing the behavioural patterns of different populations in Africa (Whiten et al. 1999, 2001). Population-specific behavioural differences are particularly evident in tool use. However, the observational nature of most field studies makes it difficult to draw definitive conclusions, as it is impossible to rule out all potential ecological or genetic explanations for behavioural variation attributed to culture (Galef 2009; Tomasello 2009). Although social transmission has been observed in captivity, with good evidence that chimpanzees can socially learn and transmit behaviours (Whiten et al. 2007; Whiten 2009), it is currently unclear to what degree this finding can be applied to chimpanzees in the wild. For example, it is possible that chimpanzees re-solve a particular problem because they operate under the same conditions every time they are confronted with it, or that they have learnt the solution through individual trial-and-error learning and not through cultural transmission (Tennie et al. 2009). Testing cultural knowledge, therefore, requires field experiments by which individuals of the same genetic background are tested with a novel problem under the same environmental conditions, thus controlling for all other potential sources of explanations.

Additionally, it is unknown to what extent wild animals understand what they are doing when they display their cultural behaviours. As such, they may well re-apply the same behaviour over and over without understanding why they do so. Recent theoretical models of ape intelligence, however, link intelligence and cultural knowledge within a general 'human-like' intelligence model (Reader et al. 2011; van Schaik and Burkart 2011). Although statistics and captive work support these models, it remains to be seen if empirical data acquired in the wild are in agreement with the predictions.

While testing one single community on its own can bring insights about the transmission of behaviours, especially as female chimpanzees generally have migrated from another group which may have different traditions (Biro et al. 2003), most studies of culture in captive apes compare two groups with different seeded behaviours (Whiten and Mesoudi 2008; Whiten 2009). Strangely, such an approach has not yet been conducted in wild animals, although purely observational comparisons between sites have been numerous (McGrew 1992; Whiten et al. 1999). Interestingly, some study sites, although close to each other, show surprising differences when compared pairwise. An overview of the Sonso community tool catalogue

shows that chimpanzees of this community appear to lack all stick-using techniques observed in other communities during food acquisition, notably the 'fluid-dip' technique that allows chimpanzees to extract liquids (water, honey) with sticks (Whiten et al. 1999). Stick use is restricted to nest building and a (apparent) play behaviour where branches are held against the body, for instance under the armpit (M. Gideon, S. Amati, personal communication). However the Sonso chimpanzees have a developed leaf technology that encompasses water sponging and body cleaning (Reynolds 2005). In comparison, chimpanzees at Kanyawara, although similarly quite limited in their tool use catalogue, use sticks during food acquisition on an habitual basis (Whiten et al. 1999). Given that these two communities are of the same subspecies, *Pan troglodytes schweinfurthii*, it is unlikely that their behavioural differences result from genetic differences, notably as *P. t. schweinfurthii* has a low genetic diversity (Goldberg and Ruvolo 1997a, b).

In this study, I conducted the first field experiment comparing two chimpanzee communities, Sonso and Kanyawara, to investigate how their cultural knowledge influenced their way of solving a simple cognitive task under identical ecological conditions. I exposed individuals of the two communities to the same task, an artificial hole drilled into a horizontal log, filled with natural honey. Honey, produced by bees of the *Apis*, *Meliponula* and *Xylocopa* genera, is found in both forests and consumed by members of both communities (Reynolds 2005, Muller & Wrangham, personal communication). Similarly to human experimental protocols adapted to apes (Haun et al. 2006a; Haun et al. 2006b), in this experiment the chimpanzees were left to find their own way of solving the task, without being trained to perform a particular action. This allowed me to study the spontaneous solutions that they might generate when confronted to this novel problem, exploring how an individual's initial knowledge would influence its selection of an action to solve the task. Secondly, I wanted to investigate if the knowledge individuals relied on to solve the task could be characterised as cultural, with a dominant solution selected by most members of the same group, potentially different from the solution chosen by another group.

## 2. Methods

### Subjects, set-up and general protocol

The experiment was conducted with the Sonso and the Kanyawara communities, following the protocol described in chapter 2. Experiments at Budongo took place between 20 February and 25 March 2009 and at Kibale between 2 and 22 April 2009. I chose to use a rectangular shape to provide a visually novel stimulus that differed from the entrance of the beehives chimpanzees naturally encounter in the wild. In another difference the hole was presented in the horizontal plane. Natural beehive entrances are usually found on the vertical sides of trunks (see Appendix D) but chimpanzees may also access the hives after the supporting trees have fallen down. In such cases, the tree is usually broken and honey is easily accessible (personal observations). Finally, I provided honey as a liquid substrate as opposed to the waxy honey naturally encountered by the chimpanzees. This accumulation of differences generated a task sufficiently different from what chimpanzees usually encounter in the forest, while conserving the basic natural features. This way I was able to ensure that individuals were not relying blindly on simple stimulus-response algorithms acquired previously for example by operant conditioning.

### Obligatory and non-obligatory experiments

Two types of hole were drilled at each site. The first was 11 cm deep with honey filled up to 6 cm below the surface. This allowed the chimpanzees to get most of the honey by only using their fingers, hence tool use was not required. Honeycombs were scattered around the hole to provide a visual cue (Fig. 4.1a). In the second experiment, the same hole was re-drilled to a 16 cm depth, with honey filled up to 10 cm beneath the surface. In this condition, it was no longer possible to access the honey with the fingers. Again, honeycombs were positioned to provide visual cues, this time covering the hole to prevent insects from exploiting the honey before the chimpanzees arrived, wild bees having started to forage into the hole at the time the second experiment started (Fig. 4.1b). This change in the setting did not cause noticeable effects on the chimpanzees who approached the hole similarly in the two experiments.

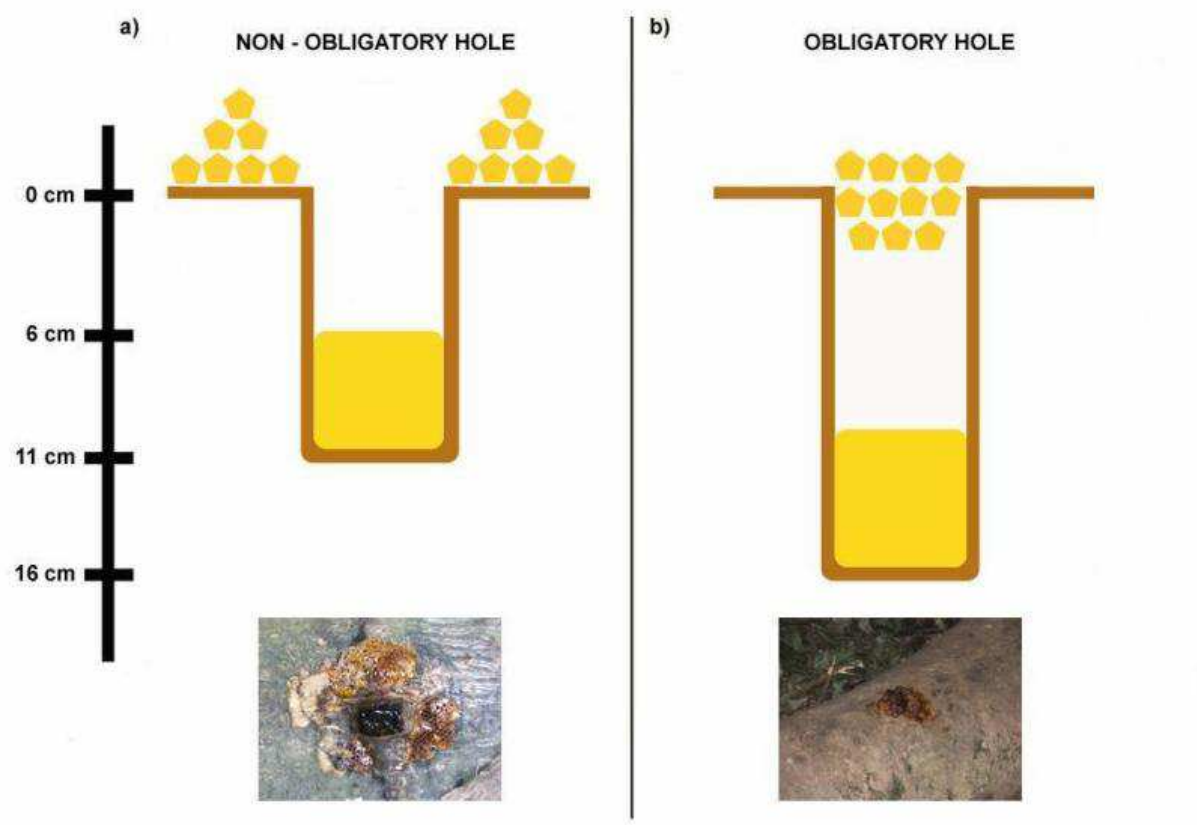


**Figure 4.1.** Schematic representation of the two experimental conditions of honey presentation: a) Experiment 1. A hole of 11 cm was drilled into a tough recently fallen log. Natural honey was filled up to 6 cm below the surface, which could be reached by inserting one or several fingers. Honey combs were placed around the entrance to attract the chimpanzees (picture taken at Sonso by T. Gruber). b) Experiment 2. The same hole was re-drilled to a depth of 16 cm and honey was filled up to 10 cm beneath the surface. Honeycombs were used to cover the entrance to the hole and prevent wild bees from entering and harvesting the honey (picture taken at Kibale by T. Gruber).

**Data analysis**

All statistical tests were calculated with SPSS v 16.0 (copyright © SPSS Inc.) except for the Freeman-Halton extension of the Fisher Test, which was calculated using the Vassar College method (http://faculty.vassar.edu/lowry/VassarStats.html). Fisher exact tests give a measurement of the difference between populations but no indication of effect strength. To estimate the size of the effect (i.e. how different the two populations were), I calculated

Goodman and Kruskal's λ, a measure of proportional reduction in error. It indicates the extent to which the modal categories and frequencies for each value of the independent variable differ from the overall modal category and frequency, i.e. for all values of the independent variable together. Values for λ range from zero (no association between independent and dependent variables) to one (perfect association between the two). λ is calculated with the equation:

$$\lambda = (\varepsilon_1 - \varepsilon_2) / \varepsilon_1$$

where $\varepsilon_1$ is the overall non-modal frequency, and $\varepsilon_2$ the sum of the non-modal frequencies for each value of the independent variable.

## 3. Results

### Community-specific tool preferences

At both sites, individuals initially showed similar responses to the artificial holes by consuming all available honeycombs. However, their subsequent behaviours differed in striking ways.

At Sonso, most individuals relied on their hands only to access the honey in both experimental conditions (Table 4.1) but some of them also used leaves (Fig. 4.2a). For the 11 cm hole, tool use was not required, but two of 13 individuals nevertheless inserted leaves to extract honey (RE and PS). In the second experiment, tool use was necessary and two further individuals of 10 in total were observed to compress leaves in their mouth to produce a leaf-sponge. One of them, a sub-adult male (HW), proceeded to extract the honey.

In comparison, at Kanyawara, most chimpanzees prepared sticks to access the honey (Fig. 4.2b; 11 cm hole: 6 of 10 individuals; 16 cm hole: 11 of 12 individuals). No individual at Kanyawara used leaf-sponges, although the behaviour is customary in the community in other contexts (Whiten et al. 1999).

**Table 4.1.** Summary of the durations of engagement with the honey-trap experiments in the Sonso and the Kanyawara communities.

| Community | ID | Age | Experiment | Mode | Use of tool | Direct engagement time | Total engagement time | Latency before first tool use | Mean time before tool use |
|---|---|---|---|---|---|---|---|---|---|
| Kanyawara | AJ | Adult | Non-Obligatory | H | No | 1307 | 1307 | n.a | n.a |
| Kanyawara | AL | Adult | Obligatory | M, S | Yes | 10 | 10 | 4 | 4 |
| Kanyawara | AT | Juvenile | Obligatory | H, M, S | Yes | 259 | 259 | 20 | 20 |
| Kanyawara | BO ¤ | Juvenile | Obligatory | H, M, S | Yes | 97 | 97 | 3 | 3 |
| Kanyawara | ES | Sub-Adult | Non-Obligatory | H, S | Yes | 1448 | 1734 | 0 | 0 |
| | | | Obligatory | H, S | Yes | 286 | | ** | ** |
| Kanyawara | EU | Juvenile | Non-Obligatory | H | No | 112 | 958 | n.a | n.a |
| | | | Obligatory | H, S | Yes | 846 | | ** | ** |
| Kanyawara | KK | Adult | Non-Obligatory | H, M, S | Yes | 260 | 260 | *** | *** |
| Kanyawara | LK | Adult | Non-Obligatory | H | No | 114 | 114 | n.a | n.a |
| Kanyawara | LR | Adult | Non-Obligatory | H, S | Yes | 446 | 948 | *** | *** |
| | | | Obligatory | H, S | Yes | 502 | | *** | 5 |
| Kanyawara | NP | Juvenile | Obligatory | H, M, S | Yes | 2899 | 2899 | 40 | 27 |
| Kanyawara | OG | Juvenile | Obligatory | H, M, S | Yes | 852 | 852 | 8 | 8 |
| Kanyawara | OT | Sub-Adult | Obligatory | H, M, S | Yes | 834 | 834 | 20 | 26 |
| Kanyawara | PB | Sub-Adult | Non-Obligatory | H, S | Yes | 296 | 296 | 88 | 88 |
| Kanyawara | PG ¤ | Adult | Non-Obligatory | H | No | 5 | 11 | n.a | n.a |
| | | | Obligatory | H | No | 6 | | n.a | n.a |
| Kanyawara | QT | Adult | Non-Obligatory | H, M, S | Yes | 1515 | 8795 | 0 | 125 |
| | | | Obligatory | H, M, S | Yes | 7280 | | *** | 7 |
| Kanyawara | TJ | Sub-Adult | Obligatory | M, S | Yes | 269 | 269 | 45 | 45 |
| Kanyawara | WL | Adult | Non-Obligatory | H, M, S | Yes | 1540 | 1540 | 34 | 25 |
| Sonso | AN | Adult | Obligatory | M | No | 30 | 30 | n.a | n.a |
| Sonso | HL | Juvenile | Obligatory | H | No | 98 | 98 | n.a | n.a |
| Sonso | HT | Adult | Obligatory | H, L | Yes | 102 | 102 | 4 | 4 |
| Sonso | HW | Sub-Adult | Non-Obligatory | H | No | 27 § | 127 | n.a | n.a |
| | | | Obligatory | H, L | Yes | 100 | | 54 | 54 |
| Sonso | KL | Adult | Non-Obligatory | H, M | No | 60 | 60 | n.a | n.a |
| Sonso | KM | Sub-Adult | Non-Obligatory | H | No | 4 | 4 | n.a | n.a |

Table 4.1. continued

| Community | ID | Age | Experiment | Mode | Use of tool | Direct engagement time | Total engagement time | Latency before first tool use | Mean time before tool use |
|---|---|---|---|---|---|---|---|---|---|
| Sonso | KN | Sub-Adult | Non-Obligatory | H, M | No | 14 | 14 | n.a | n.a |
| Sonso | KS | Juvenile | Non-Obligatory | H | No | 60 | 60 | n.a | n.a |
| Sonso | KU | Adult | Non-Obligatory | H, M | No | 105 | 105 | n.a | n.a |
| Sonso | MK | Juvenile | Obligatory | H | No | 45 | 45 | n.a | n.a |
| Sonso | ML | Adult | Obligatory | H | No | 45 | 45 | n.a | n.a |
| Sonso | NB | Adult | Obligatory | H, M | No | 478 | 478 | n.a | n.a |
| Sonso | NR | Sub-Adult | Non-Obligatory | H, M | No | 108 | 170 | n.a | n.a |
| | | | Obligatory | H, M | No | 62 | | n.a | n.a |
| Sonso | NT | Juvenile | Obligatory | H | No | 493 | 493 | n.a | n.a |
| Sonso | PS | Sub-Adult | Non-Obligatory | H, M, L | Yes | 106 | 106 | *** | *** |
| Sonso | RE | Sub-Adult | Non-Obligatory | H, M, L | Yes | 279 | 279 | 61 | 61 |
| Sonso | SB | Adult | Obligatory | H | No | 75 | 75 | n.a | n.a |
| Sonso | ZG | Sub-Adult | Non-Obligatory | H, M | No | 30 | 30 | n.a | n.a |
| Sonso | ZK | Juvenile | Non-Obligatory | H | No | 50 | 50 | n.a | n.a |
| Sonso | ZL | Sub-Adult | Non-Obligatory | H | No | 194 | 194 | n.a | n.a |
| Sonso | ZM | Adult | Non-Obligatory | H, M | No | 105 | 105 | n.a | n.a |

Data points are sorted per individuals and community. Individuals are presented in alphabetical order. Several individual engaged with the holes in the two experiments. Time is given in seconds. For each individual, the community of origin (Sonso or Kanyawara) and age class is given (adult, sub-adult, juvenile). Infants were not taken into account, as they merely played with the hole without attempting to acquire the honey. Measurements were taken of mode of contact with the hole by hand (H), mouth (M) or tool (S: stick, L: leaves), excluding visual information acquired by gaze. For each individual and setting (deep 16 cm hole; shallow 11 cm hole) tool use was scored (yes/no). Total time engaging with the hole is given for both settings separately and combined. Latency to tool manufacture is calculated from an individual's first engagement with the hole. All cases where individuals had a previous knowledge of the hole were excluded. *: individual manufactured tool but did not use it. **: delay in the onset of the automatic video camera did not allow exact time measures before taking a tool. ***: individuals with prior knowledge of the hole (either with a previous setting or a previous non-tool engagement) excluded from the analysis. ¤: individuals missing a hand because of a snare. §: engagement with the combs only, not with the hole.


**Figure 4.2.** Tools used by the chimpanzees during the honey acquisition. a) Wadges of leaves manufactured by chimpanzees at Sonso during experiment 1. b) A selection of sticks manufactured by chimpanzees at Kanyawara during experiment 1 and 2.

**Speed of tool selection in the two communities**

The Kanyawara chimpanzees engaged significantly longer (N = 18, mean time of 1177 s, SD = 2044 s) with the two holes than the Sonso chimpanzees (N = 21, mean time of 127 s, SD = 135 s) (Mann-Whitney test, U = 70, p = 0.001), but this difference could not explain why Sonso chimpanzees never used sticks. As time before manufacturing a tool did not differ significantly between the two conditions in Kanyawara (shallow hole, N = 4, mean = 30.5, SD = 41.5; deep hole, N = 7, mean = 20, SD = 15.6; Mann-Whitney test, U = 16, p = 0.704), I pooled the data and excluded cases where an individual had engaged previously with the hole before manufacturing a tool. The mean Kanyawara duration from first encounter to choosing a tool was 23 s (N = 11, range 0 – 88 s). Most chimpanzees at Sonso spent more than 23 s engaging with the hole, so that they would have had sufficient time to select a stick. Moreover, the three Sonso individuals who produced tools during their first engagement with the hole did so in the time range of the Kanyawara chimpanzees (N = 3; range 4 – 61 s).

### Tool preferences are markers of community membership

Overall, there was significantly more tool use at Kanyawara than Sonso in both the 11 cm (non-obligatory) shallow (Fisher exact test, $p < 0.05$) and the 16 cm (obligatory) deep condition ($p = 0.002$). Using the Freeman-Halton extension of the Fisher test (Freeman and Halton 1951), I found that the overall distribution of the three categories of responses (no tool use, sticks, leaves) was significantly different from the null hypothesis, i.e., the two populations being identical in their techniques to access the honey ($p < 0.01$ and $p < 0.001$, respectively), providing statistical evidence that Kanyawara and Sonso chimpanzees responded in a group-specific manner. To assess the size of this difference, I calculated the Lambda value for predicting tool use (yes or no) and for predicting the response category (no tool, stick, leaf). The Lambda test is a non-parametric variable that gives the proportional reduction in error when group membership is used as a variable to predict behaviour (Goodman and Kruskal 1979). For predicting tool use, I obtained lambda values of 0.400 (shallow condition) and 0.857 (deep condition). For predicting the response category, I obtained lambda values of 0.6 and 1 (see methods). Although in the shallow condition the range of response choices was larger than in the deep condition, both lambda values demonstrated that group identity was a strong predictor of behaviour in both conditions.

## 4. Discussion

### Suitability of field experiments to study cultural variation

The systematic description of community-specific patterns of behaviours in chimpanzees and other animals (Whiten et al. 1999; van Schaik et al. 2003) has not convinced all sceptics that this variation may be comparable to human cultural variation, as ecological and genetic factors may be responsible for the observed variation rather than cultural factors (Laland and Janik 2006; Galef 2009; Tomasello 2009). However, carefully selecting closely related populations and using experimentally controlled areas allows researchers to minimise genetic differences and to control for the ecological influences that could drive chimpanzees to use certain behaviours rather than others. From a methodological point of view, the results I presented in this chapter thus demonstrate that, by using simple cognitive tests to which there are several solutions, the disparate influences that affect behaviour can be studied

systematically in the wild, depending on the populations selected for the experiment. For instance, one could select two populations with the same genetic origin but with different environmental influences during ontogeny (for instance sanctuary vs. mother-reared) to study the influence of the social or physical environment on the development of the behaviours. To my knowledge, this experiment is the first to compare two genetically close populations of the same subspecies (Goldberg and Ruvolo 1997b) with the same task allowing genetic, environmental and task-related influences to be controlled for, allowing me to study how chimpanzee's individual knowledge helped them to solve a novel problem. By using a standardised hole, filled with the same type and amount of honey, under the same environmental conditions, any differences in observed behaviour are most parsimoniously attributed to the individuals' prior learning histories or, more specifically, the differences in their cultural backgrounds (Whiten et al. 1999, 2001). Although this protocol does not test for cultural differences *per se* (as it does not study social learning processes for instance), the results, based on the comparison of two different communities, allow one to compare how individuals performed within as well as between communities. Therefore, the statistical analysis of the result may find potential community-specific ways of solving the task. In the particular case of the experiment presented here, cultural differences appear as the most plausible explanation (see below). Field experiments of this kind, when combined with the necessary observational studies and supported by more controlled studies in the laboratory, can therefore provide a robust test to systematically compare cultural differences in wild animals.

**Chimpanzees rely on their general knowledge when confronted with new tasks**

From a cognitive point of view, my results suggest that chimpanzees rely heavily on their previous knowledge to solve a novel foraging problem. Kanyawara chimpanzees occasionally attempt to acquire small amounts of honey (ca. 1-5 mg) available in the nests of solitary carpenter bees (*Xylocopa* spp.). Such attempts always involve a probing stick used to obtain the waxy honey. They continued to use this technique when the food was encountered in the spatially and visually novel setting of my field experiment. In contrast, the Sonso chimpanzees do not use tools to access food other than water and, consequently, their first approach to the problem was to use their fingers. The Sonso chimpanzees produce leaf-sponges to retrieve water from holes in trees, and some individuals applied this technique to

the novel problem of the experimental situation. The reason why they used leaf-sponging for honey acquisition is however unclear. The fact that they consumed the combs beforehand, possibly perceived the smell of honey and perceived the presence of bees, makes it improbable that they anticipated finding water in the artificial hole. Additionally, several individuals were observed wiping their hands vigorously on the log after contacting the honey with it, leaving no doubt that they did not mistake it for water. The fact that they relied on leaf-sponging is evidence that stick use in the context of food acquisition is absent in the Sonso chimpanzees. Leaf-sponging is unlikely to be suitable for honey extraction from natural beehives as no other community has ever been observed using this behaviour in this context. This is particularly true as honey is usually embedded in waxy combs found deep inside the hive and protected by the bees. Thus, if they had had stick use in their repertoire, the Sonso chimpanzees would have probably used this technique, which is related to honey acquisition in chimpanzee daily life, rather than leaf-sponging, as the Kanyawara chimpanzees did. It is noteworthy to mention that the latter nonetheless use leaf-sponges to collect water on a habitual frequency but did not use this technique to get the honey. Additionally, the Sonso individuals produced leaf-sponges at the same speed as the Kanyawara individuals produced sticks. This suggests that they relied on this technique as if it was natural to them to use it with honey. Whether they considered if stick use could be a suitable alternative is unknown. In other words, although these data show that chimpanzees clearly rely on what they know when confronted with a novel feature in their environment, they are limited in exploring if chimpanzees are analysing this knowledge and selecting the most suitable solution to solve a certain problem when different possibilities are available. Chapter 5 will explore such questions.

**Community-specific behaviours constitute a reservoir of cultural knowledge**

The strong segregation of behaviours in this experiment (no stick use in Budongo, no leaf use in Kanyawara) suggests that the knowledge individuals relied on when solving the task was not only their own knowledge, but more generally their group's knowledge. It is theoretically possible that the stick use by the Kanyawara chimpanzees is the result of individual rather than social learning. For instance, they could have come up with stick use as an ad hoc solution to the task, experimenting by trial-and-error learning. Secondly, every individual who participated in the experiment may have developed stick use on its own prior to the

experiment, because of environmental constraints, and subsequently transferred its knowledge to the task I presented. Although my study does not address the previous learning history of our animals, a number of points make it unlikely that individual learning would be the only mechanism at work. First, the speed of choice of the tool in both communities suggests that ad hoc individual learning on a trial-and-error basis is an unlikely explanation for the observed differences. Affordance learning of the task can also be ruled out by the fact that the physical properties of the task were kept identical, due to the design of the experiment, yet the chimpanzees responded in community-specific ways. Finally, when considering individuals' prior learning history, the ecological and genetic similarities between the two communities hardly explain a complete segregation of the behaviours chosen by the individuals. Given that chimpanzees in both forests are exposed to the same species of bees, they are exposed to the same stimuli that could trigger naturally the development of stick use in the context of honey foraging. The individual learning hypothesis would predict that individuals in both groups should be equally likely to learn stick use to obtain natural honey; however, that was not the case. Because of all these reasons, it is more likely that their decisions were based on cultural knowledge in line with the evidence from captivity (Bonnie et al. 2007; Whiten et al. 2007). Finally, it should be noticed that individual and social learning are not necessarily incompatible. For instance, in the theory of programme-level imitation, while the general programme is thought to be acquired through a social influence, each step could be mastered through individual learning (Byrne and Russon 1998; see chapter 7 for a general discussion).

Interestingly, the behavioural results obtained with these experiments also reflect subtle differences in dietary habits between the two communities (Nishida et al. 1983; Wrangham et al. 1994). The Kanyawara chimpanzees eat *Apis* honey about once per month and unsuccessfully try to obtain honey at a similar rate (Kibale Chimpanzee Project, unpublished data, 1991-2001). By comparison, honey consumption is rare in Sonso, but this has nothing to do with the anti-predator behaviour of the bees, which fiercely attack chimpanzees at both sites (Gruber, personal observations). In my experiment, Kanyawara individuals engaged longer with the hole, and revisited the experimental spot regularly when feeding in the vicinity. At Sonso honey consumption appeared to be much more opportunistic, coinciding with feeding at a nearby *Raphia farinifera* tree (Reynolds et al. 2009). Honey consumption would thus appear more traditional at Kanyawara, when it would be more opportunistic in

Budongo. As such, the results of this experiment suggest that diet preferences are at stake and that they are possibly cultural, such as has been described in orangutans (Jaeggi et al. 2010a).

In conclusion, three points can be made. Firstly, as argued above, the fact that all the chimpanzees reacted in a community-specific way supports a culturally-based rather than individual acquisition of the behaviour. These results generally agree with the accepted definition of culture as a community-specific set of behaviours that an individual is exposed to and can socially learn from (Fragaszy and Perry 2003a). According to this view, the Sonso chimpanzees do not use sticks during feeding because they have never seen another chimpanzee using sticks in this context, but once someone invents the technique, it may spread through the community through socially-aided processes (Biro et al. 2003; Nishida et al. 2009). Secondly, these experiments do not show how individuals originally acquired their set of foraging behaviours, only how individuals apply their knowledge when confronted with novel problems. Therefore, although the cultural characteristic is supported through statistics, it does not bring any proof of social learning and thus still faces the psychological criticisms, although it brings answers to the biological ones. As a final point, this study highlights the fact that the 'exclusion method', commonly used to identify cultural differences among populations (Krützen et al. 2007), is suitable to identify cultural variants. However, although both chimpanzee populations have been observed to use leaf-sponges, considered a chimpanzee universal by this method, only the Sonso community applied this technique to the experimental condition. This suggests that the contextual use of a behaviour should be taken into account when comparing cultural differences between populations, privileging a multi-modal approach to the cultural problem (Byrne et al. 2004).

# Chapter five: Culturally-biased chimpanzees do not learn tool use through emulation

Results from this study are accepted for publication in:

**Gruber, T.**, Muller, M.N., Reynolds, V., Wrangham, R.W. & Zuberbühler, K. (In press) Community-specific evaluation of a tool affordances and potential learnt irrelevance in wild chimpanzees. Scientific Reports.

## Summary

Animal cultures are usually defined as socially transmitted community-specific behaviour patterns. This definition thus describes surface behaviours without addressing underlying cognitive processes. Human cultures manifest themselves similarly but are the product of socially acquired ideas that shape how individuals interact with their environment. As a consequence, many authors argue that chimpanzee cultures fall short in comparison with human cultures, which are generally defined as sets of ideas and beliefs. Additionally, chimpanzees are believed to acquire their cultural behaviours through emulation, a learning mechanism in which they attempt to replicate an environmental effect rather than a demonstrator's action. In this chapter, I address both questions with a set of field experiments conducted with the Sonso and Kanyawara communities. I provided members of the two communities with a suitable tool to solve the honey-trap experiment in its obligatory condition. The results revealed significant differences in how individuals considered the affordances of the tool when solving the task. Results suggest that individuals segregated the world into salient features in community-specific ways and possibly experience a cultural bias in their cognition. I discuss how this cultural bias may result from a cultural override such as experienced by humans during ontogeny. Overall, these results suggest that culture shapes the way chimpanzees see the world, and that chimpanzee cultures should be redefined as sets of ideas rather than behaviours, similar to how human cultures are commonly described.

## 1. Introduction

Reports of large-scale community-specific behaviour differences in wild chimpanzees have led to the provocative hypothesis that culture, which was thought to be a landmark of mankind, may be more widespread in the animal kingdom (Boesch 2003; McGrew 2009). Unsurprisingly, this conclusion has remained highly controversial, for both empirical and theoretical reasons. For example, a major weakness of this claim is the nature of the empirical evidence, which is largely based on observational data and questionnaires from the different study sites (Galef 2009; Tomasello 2009). However, even though the behavioural diversity is nowadays accepted by most sceptics, it is often thought that chimpanzee cultural behaviours are acquired through individual trial-and-error learning that depends on the ecological conditions an individual is facing (Call and Tennie 2009; Galef 2009; Tennie et al. 2009). For instance, it has been argued that an infant chimpanzee that sees the wind moving a log and exposing ants will learn the same as if it had witnessed its mother rolling the log, subsequently developing the behaviour on its own through a mechanism named 'emulation' (Tomasello 1990, 1996). Although the definitions of emulation have varied since the term was proposed by Tomasello (1990), the most recent version focuses on reproducing the result rather than the action, and *in fine*, leaves little space for a social influence (Tomasello 1996; Tennie et al. 2009). As illustrated by Tomasello, a chimpanzee may learn as much from the wind as from its mother, suggesting that social variables are irrelevant. Emulation has been tested in captivity, notably through ghost experiments, and results suggest that chimpanzees indeed rely on emulation learning in simple experimental designs (Hopper et al. 2008; Tennie et al. 2010). However, their ultimate failure in more complicated designs involving tool use was attributed to the absence of model (Hopper et al. 2007). What social learning mechanism chimpanzees rely on in the wild is unknown.

Another widely shared belief is that even if chimpanzees or other animals are granted with culture, this 'animal culture' has no real impact on the daily lives of animals, much in contrast to humans (Tennie et al. 2009). The impact of culture on human cognition and behaviour is well established, both theoretically and empirically (Levinson et al. 2002; Haun et al. 2006b; Chiao and Ambady 2007; Gentner 2007; Casasanto 2008; Haun and Rapold 2009). Cultural differences have even been found at the neural level, with different brain regions being activated in culturally-specific ways during a particular task (Han and Northoff

2008). Human cognition is thus heavily influenced by a 'cultural override' that develops during ontogeny (Haun et al. 2006b). While conformity appears to occur in chimpanzees (Whiten et al. 2005), it is unknown whether similar effects of 'cultural overrides' also govern animal cognition during development. The current definitions of animal culture, which put the emphasis on behavioural variation, do not indeed include the cognitive dimension found in the human literature. Although recent models of animal intelligence linking cultural knowledge and intelligence use the word 'skills' (e.g. van Schaik and Burkart 2011), which includes a deeper cognitive dimension than behaviour, the cognitive dimension of cultural variants or the way they impact on animals' cognition have found little echo in recent syntheses on animal cultures (Fragaszy and Perry 2003a; Laland and Galef 2009b).

Here, I addressed both questions by exposing wild chimpanzees to a series of field experiments. Firstly, I wanted to know if different populations of chimpanzees had a different perception of the same tool, notably in its perceived affordances to solve a particular task. Secondly, I wanted to explore if exposing naïve chimpanzees to a novel technique and allowing them to experience the physical action of an unknown tool-using action (stick use) would make them develop this behaviour through affordance learning, a key component of emulation (Tomasello 1996). Based on the results described in chapter 4, another hypothesis was that chimpanzees could be strongly constrained by previous cultural knowledge to the point of being unable to understand a novel object as a tool. In that case, demonstrations of the technique by a conspecific may be the only way for an individual to learn it. To address these two questions, I presented members of the Sonso and Kanyawara communities with an identical task: extracting honey trapped in a 16 cm deep hole with a 5x4 cm opening of a portable log of 50 cm length and 25 cm width (replicating the obligatory condition of the previous experiments). However, this time, in the critical test condition, I provided a suitable tool next to the hole, a 40 cm branch of an *Alstonia* shrub, with all leaves removed for half of its length (Fig. 5.1). In chapter 4, I have documented that individuals of these two communities differ in their tool preferences for using leaves or sticks respectively, to extract honey in this task with no obvious efficiency differences. However, while in Kanyawara, only 3 of 17 individuals tested did not manufacture tools to access honey, in Sonso, only 4 of 24 found a tool solution to the problem. Although manufacturing a tool was not required in the first experiment (as most honey was accessible with fingers), it was mandatory in the second experiment (obligatory condition), as the honey was too far to reach with fingers. Nonetheless, only 2 Sonso individuals who participated in this experiment produced a tool (a

leaf-sponge); the 9 others remained unsuccessful. Given my two questions, in my first experiment, I wanted to investigate chimpanzees' choice selection process when provided with a multi-usage tool. In the follow-up experiment, given that most Sonso individuals had still not found a tool solution to solve the honey extraction problem, I exposed them to the solution found by the Kanyawara chimpanzees to see if the non-tool users would adopt this technique rather than staying unsuccessful.

## 2. Methods

### Experimental conditions

Contrary to chapter 4, this set of experiments only confronted chimpanzees with the 16 cm deep hole, but under different conditions: baseline, experiment 1 and 2. In Budongo, data were collected between September 14, 2009 and July 17, 2010. In Kibale, data were collected between August 20 and 24, 2010.

*Baseline condition (Sonso only)*

Chimpanzees were allowed to engage freely with the hole, with no tool present. In chapter 4, Kanyawara chimpanzees had spent more time engaging with a similar apparatus, and they produced a tool after an average engagement time of 20 s in the obligatory experiment. This additional exposure might have given more time to individuals to select stick use as an option to extract honey in Kanyawara, a situation that I wished to control for in Sonso. This baseline condition allowed the Sonso chimpanzees to match the Kanyawara individuals in terms of engagement time, reproducing the obligatory condition of chapter 4.

*Experiment 1*

Chimpanzees at both sites were allowed to engage with the hole and a tool, the 'leafy stick' (Fig. 5.1), was proposed half-way between the hole and either edge of the log, randomly among trials. This tool consisted of a 40 cm branch of *Alstonia ssp*, a common shrub in

Budongo and Kibale forests, stripped of leaves on the lower 20 cm of its length so that it could be used either as a 'stick' (by inserting the bare end), as a 'brush' (by inserting the leafy end) or as a 'leaf-sponge' (by removing and chewing its leaves and inserting the resulting sponge). Skilled tool-users managed to access the honey in less than 10 minutes, by inserting the leafless end of the tool ('stick') or by removing the leaves and chewing them into a wedge ('sponge'), and the two techniques appeared similar in efficiency (I could not test this statistically because honey was rarely consumed entirely in Sonso as leaf-spongers were often displaced by more dominant individuals, but for those who finished the honey, they did so within the range of the Kanyawara individuals).

With this experiment, I wanted to study if chimpanzees of different communities would find a particular part of the tool salient to use for the task. If a certain part of the tool had a particular affordance for this task, one would expect chimpanzees of both communities to use it preferentially to dip for honey. On the contrary, if each community had specific preferences, this could suggest a community cultural bias in apprehending the environment.

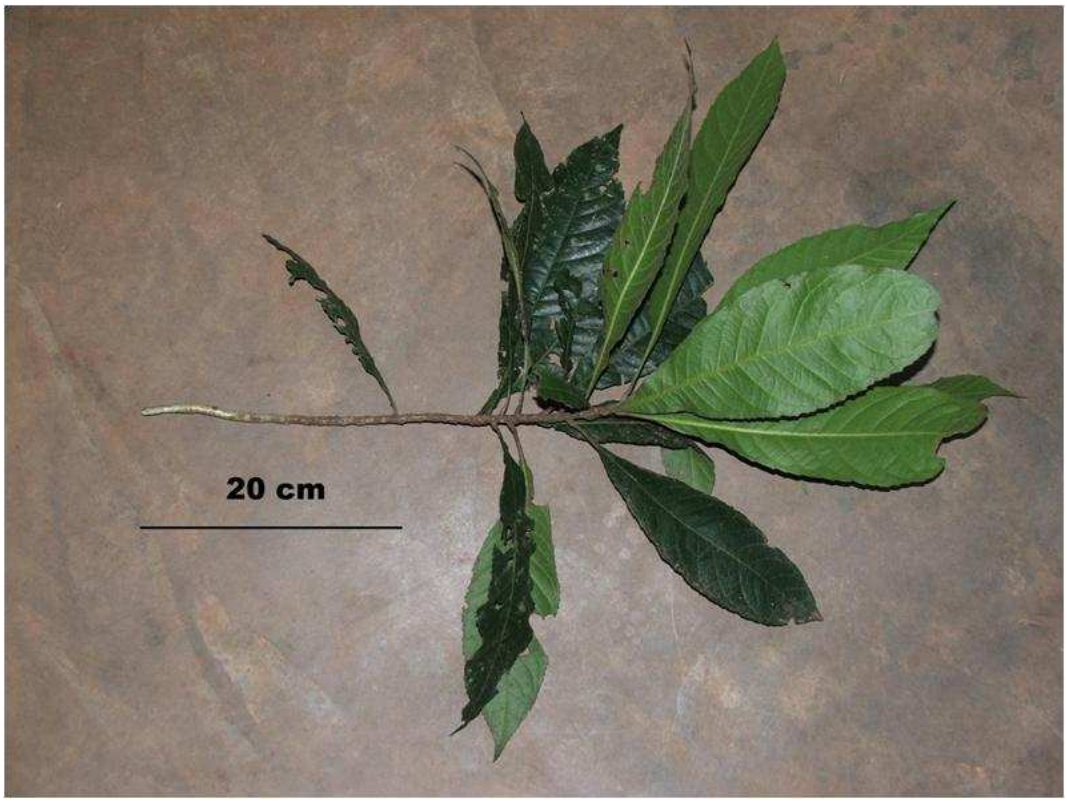


**Figure 5.1.** The tool provided during the experiments: the 'leafy stick', a 40 cm branch of *Alstonia ssp*, stripped of leaves on the lower 20 cm of its length (picture by T. Gruber).

*Experiment 2 (Sonso only)*

In this experiment, I only tested the Sonso individuals, because most of them ignored the leafy stick and remained unsuccessful in attempting to get honey. I wanted to test directly the emulation hypothesis as proposed by Tennie and colleagues (Tennie et al. 2009) which states that "*nut crackers and termite fishers leave their tools and detritus behind, and in the right place, which makes the learning of their offspring and others much easier"*(p. 2406). Consequently, I presented the leafy stick directly inserted into the hole before chimpanzees' arrival. This type of presentation was designed to make the alternative features of the tool particularly obvious because, when removing the tool from the hole, the honey would drip from the stick-part. For individuals who had previously responded with leaf-sponging to the problem, i.e. experienced tool users, I was interested in determining whether they would consider these alternative functions of the tool, and favour any of them over their existing leaf-sponging technique in subsequent attempts. For all other individuals, i.e. those who had never been observed manufacturing leaf-sponges or using other tools to extract honey, I was interested in whether this manipulation would make them learn stick use, as the emulation hypothesis proposes.

As chimpanzees initially did not show much interest in the tool in the initial setting of this experiment ((a): wooden part inside the hole, free of the combs, in contact with honey), I tested four other settings to increase their interest towards the stick-part of the tool: (b): wooden part through the comb and inside the hole, in contact with honey; (c): leafy part inside the hole, in contact with honey; (d) wooden part inside a 3x3 cm hole; (e): leafless, chewed 40 cm stick; the stick was chewed by an adult baboon who engaged with the log before chimpanzees; see Appendix E. Each of these settings showed a different use of the stick which could make its properties salient ((b): stick can pierce combs; (c): stick can be used as a brush; (d): hole too small to insert a leaf-sponge; (e): leaves are not necessary to get honey), and I wanted to know if any of these could drive chimpanzees to develop stick use on a one time exposure basis. Realistically, wild individuals are not expected to encounter sticks left in natural bee hives more than once in their life, if ever. Thus, if affordance learning, without any social influence, were to occur naturally as the mechanism responsible for stick use appearance, one single exposure would have to be enough to trigger the development of the behaviour.

Not all individuals engaged with the hole in the same settings. In field experiments of this kind, it is impossible to select the participants, as they may show up at the experimental location (fruiting tree) or not. Additionally, to keep the interference as low as possible, I never exposed the same group for more than one week to experiments. Finally, I could not conduct the complementary experiment at Kanyawara (a leaf-sponge in the hole): leaves are folded and chewed to produce the final sponge, a manipulation that I could not perform due to the inherent risks of disease transmission.

**Relevance of the comparative analysis and statistics**

To analyse my results, I compared the results obtained in these experiments with results obtained in chapter 4. Specifically, in order to compensate for the impossibility to control for subject participation, I compared the amount of time chimpanzees spent engaging with the hole in the two communities. Comparing total duration of engagement with the hole, and especially duration before which they manufacture a tool, is the most accurate way of controlling for individual differences in participation. In chapter 4, I found that in the obligatory condition, Kanyawara chimpanzees started manufacturing tools on average 20 s after their first contact with the apparatus (N = 11 individuals). Thus, in this chapter, I only considered for comparison purposes individuals who engaged with the hole for 20 s or more in the different conditions. All statistical tests were calculated with PASW Statistics v. 18.0.

## 3. Results

**Baseline**

Sonso individuals were given more time to engage with the apparatus with no tool provided. Following this baseline condition, Sonso individuals equalled Kanyawara individuals in terms of engagement time ($N_{Kanyawara}$ = 14, $N_{Sonso}$ = 29, Mann-Whitney test, U = 130, p = 0.058, excluding QT in Kanyawara as an outlier; Table 5.1). No Sonso chimpanzee used or produced a stick during this condition, but three individuals manufactured leaf-sponge tools to access honey.

**Experiment 1**

In Sonso, 21 individuals participated in the experiment; 17 of 21 (81.0%) interacted with the apparatus for more than 20 s. Three of 21 (14.3%) seized the tool provided. All proceeded to detach the leaves with their lips, discard the stick and roll the leaves in their mouths to produce a sponge. The remaining 18 individuals ignored the tool, but two of these (11.1%) manufactured a leaf-sponge from the surrounding vegetation.

In Kanyawara, 12 individuals participated in the experiment; 10 of 12 (83.3%) engaged with the apparatus for more than 20 s. Five of 12 (41.7%) seized the tool, and all proceeded to insert the bare end of the stick to acquire the honey. Three of 5 removed and discarded the leafy part from the tool to work with the resulting stick but none manufactured a leaf-sponge. The remaining 7 individuals ignored the tool but 4 of these (57.1%) manufactured a stick tool from the surrounding vegetation.

**Table 5.1.** Summary of the durations of engagement with the apparatus and use of tools of chimpanzees at Sonso and Kanyawara during baseline and experimental condition 1.

| | | | BASELINE | | | | | EXPERIMENTAL | |
|---|---|---|---|---|---|---|---|---|---|
| Community | ID | Age Class | Chap 4 (s) | Tool Chap 4 | Baseline | Tool | Total (s) | Exp. Cond. (s) | Tool |
| Kanyawara | AL | Adult | 10 | Stick | 128 | Stick | 138 | x | x |
| Kanyawara | AT | Juvenile | 259 | Stick | x | x | 259 | x | x |
| Kanyawara | AZ | Juvenile | x | x | 460 | Stick | 460 | x | x |
| Kanyawara | BO | Juvenile | 97 | Stick | x | x | 97 | x | x |
| Kanyawara | ES | Sub-Adult | 286 | Stick | x | x | 286 | x | x |
| Kanyawara | EU | Juvenile | 846 | Stick | x | x | 846 | x | x |
| Kanyawara | KK | Adult | x | x | 72 | No | 72 | x | x |
| Kanyawara | LK | Adult | x | x | x | x | 0 | 4 | No |
| Kanyawara | LR | Adult | 502 | Stick | x | x | 502 | x | x |
| Kanyawara | NP | Sub-Adult | 2899 | Stick | x | x | 2899 | 347 | Stick, LS-Stick |
| Kanyawara | OG | Juvenile | 852 | Stick | 83 | Stick | 935 | 95 | Stick |
| Kanyawara | OT | Sub-Adult | 296 | Stick | 56 | Stick | 352 | 15 | LS-Stick |
| Kanyawara | OU | Adult | x | x | x | x | 0 | 179 | Stick |
| Kanyawara | PG | Adult | 6 | No | 43 | No | 49 | 29 | No |
| Kanyawara | QT | Adult | 7280 | Stick | x | x | 7280 | 735 | LS-Stick |
| Kanyawara | TG | Adult | x | x | x | x | 0 | 545 | Stick |
| Kanyawara | TJ | Adult | 1540 | Stick | x | x | 1540 | 54 | Stick |
| Kanyawara | TS | Juvenile | x | x | x | x | 0 | 56 | No |
| Kanyawara | TT | Juvenile | x | x | 44 | Stick | 44 | 3106 | Stick, LS-Stick |
| Kanyawara | WL | Adult | x | x | x | x | 0 | 649 | Stick, LS-Stick |
| Sonso | AN | Sub-Adult | 30 | No | x | x | 30 | x | x |
| Sonso | FD | Sub-Adult | x | x | 5 | No | 5 | x | x |
| Sonso | FK | Juvenile | x | x | 10 | No | 10 | x | x |
| Sonso | HL | Sub-Adult | 98 | No | x | x | 98 | x | x |
| Sonso | HT | Adult | 102 | Leaves | x | x | 102 | x | x |
| Sonso | HW | Adult | 100 | Leaves | 281 | No | 381 | 434 | LS-Sponge |
| Sonso | JT | Juvenile | x | x | 121 | No | 121 | 198 | Leaves |
| Sonso | KA | Juvenile | x | x | 20 | No | 20 | 274 | Leaves |
| Sonso | KE | Sub-Adult | x | x | 10 | No | 10 | x | x |
| Sonso | KL | Adult | x | x | 5 | No | 5 | x | x |
| Sonso | KM | Juvenile | x | x | x | x | 0 | x | x |
| Sonso | KR | Juvenile | x | x | 30 | No | 30 | 192 | No |

| (continued) | | | BASELINE | | | | | EXPERIMENTAL | |
|---|---|---|---|---|---|---|---|---|---|
| Community | ID | Age Class | Chap 4 (s) | Tool Chap 4 | Baseline | Tool | Total (s) | Exp. Cond. (s) | Tool |
| Sonso | KS | Juvenile | x | x | 235 | Leaves | 235 | x | x |
| Sonso | KT | Adult | x | x | x | x | 0 | 44 | No |
| Sonso | KU | Adult | x | x | x | x | 0 | x | x |
| Sonso | KW | Adult | x | x | 78 | No | 78 | 83 | No |
| Sonso | KY | Adult | x | x | 335 | No | 335 | 37 | No |
| Sonso | KZ | Adult | x | x | 225 | No | 225 | 40 | No |
| Sonso | ML | Adult | 45 | x | x | x | 45 | x | x |
| Sonso | MN | Juvenile | 45 | x | x | x | 45 | x | x |
| Sonso | MS | Adult | x | x | 335 | No | 335 | 740 | No |
| Sonso | NB | Adult | 478 | No | 1069 | No | 1547 | 387 | No |
| Sonso | NK | Adult | x | x | x | x | 0 | 15 | No |
| Sonso | NR | Sub-Adult | 62 | No | 329 | No | 391 | 50 | No |
| Sonso | NT | Juvenile | 493 | No | 1245 | Leaves | 1738 | 685 | LS-Sponge |
| Sonso | OK | Adult | x | x | x | x | 0 | x | x |
| Sonso | PS | Sub-Adult | x | Leaves | x | x | 0 | x | x |
| Sonso | RE | Sub-Adult | x | Leaves | x | x | 0 | 119 | No |
| Sonso | RS | Sub-Adult | x | x | 1082 | Leaves | 1082 | 142 | LS-Sponge |
| Sonso | SB | Adult | 75 | No | 285 | No | 360 | x | x |
| Sonso | SE | Adult | x | x | 45 | No | 45 | x | x |
| Sonso | SM | Adult | x | x | 45 | No | 45 | x | x |
| Sonso | SQ | Adult | x | x | 34 | No | 34 | 74 | No |
| Sonso | TK | Adult | x | x | 267 | No | 267 | x | x |
| Sonso | VR | Sub-Adult | x | x | 115 | No | 115 | 233 | No |
| Sonso | WL | Adult | x | x | 102 | No | 102 | x | x |
| Sonso | ZD | Juvenile | x | x | 33 | No | 33 | x | x |
| Sonso | ZF | Adult | x | x | 18 | No | 18 | 7 | No |
| Sonso | ZG | Sub-Adult | x | x | 119 | No | 119 | x | x |
| Sonso | ZK | Juvenile | x | x | x | x | 0 | 4 | No |
| Sonso | ZL | Adult | x | x | 287 | No | 287 | 22 | No |
| Sonso | ZM | Adult | x | x | 25 | No | 25 | 8 | No |

The baseline is composed of two sets of data; Chap 4: time spent engaging with the hole by Sonso and Kanyawara individuals in the previous study (cf chapter 4) and use of a tool (Stick or Leaves) or not (No); Baseline: baseline from this study in Sonso (plus individuals in Kanyawara who engaged with the hole when the leafy stick was absent), and use of a tool or not. In experimental condition, two kinds of tool were available: 'Stick/Leaves': any stick/leaves removed from the surrounding vegetation other from the leafy stick to access honey; 'LS-Stick/Sponge': any stick/leaves manufactured from the leafy stick (LS), or leafy stick used without modification to access honey; 'No': no tool use observed.

**Experiment 2 (Sonso only)**

Twenty individuals engaged with the apparatus in at least one of the four conditions; 15 (75.0%) did so for more than 20 s. 15 of 20 individuals (75.0%) interacted with the provisioned tool, but no one used the tool to extract honey: two individuals simply touched the tool; three touched and retrieved the tool, but then discarded it without further signs of interest. Ten removed the tool to smell the honey-covered part of the tool (6 of 10) or to consume the honey from it (4 of 10), either from the bare stick (N = 1; condition a) or from the 'brush' (N = 3; condition c; Table 5.2). All individuals subsequently discarded the stick. Finally, 5 of the 20 individuals ignored the stick completely, but instead inserted one of their hands into the hole. After these initial interactions, 19 of 20 individuals continued to probe (unsuccessfully) with their hands, or they simply walked away. One of 20 individual manufactured a leaf-sponge to extract honey. In sum, although I presented the experimental tool in a way that revealed its additional functional properties in retrieving honey, no Sonso chimpanzee was able to perceive these features. The striking result of this experiment was that none of the non-tool users discovered stick use or any means to access honey, thus staying unsuccessful in their attempts to obtain honey. None of the leaf-spongers responded to the tool's alternative functions either.

**Table 5.2.** Summary of the durations of engagement with the apparatus and reactions to the leafy stick from Sonso chimpanzees during experimental condition 2.

| ID | Age Class | Duration (s) | Setting | Reaction | Action |
|---|---|---|---|---|---|
| HT | Adult | 12 | d | Retrieves leafy-stick but discards without smelling it. | Grab |
| HW | Adult | 109 | a, b, c | Only shows interest in b: steals combs plugged on the stick; and c: Licks the honey from the leaves. In any case, discards the stick afterwards. | Lick |
| KA | Juvenile | 674 | c, d, e | d: Discards the stick without smelling it. e: Smells the naked extremity of the leafy-stick then discards. c: Smells the leaves but discards the leafy-stick and starts manufacturing a leaf-sponge. | Smell |
| KE | Sub-Adult | 122 | d | Smells the naked extremity of the leafy-stick but discards it. | Smell |
| KM | Juvenile | 50 | c | Smells and licks the leaves but then discards the stick. | Lick |
| KR | Juvenile | 13 | d | Observed her mother retrieving the stick from 5 m high. No interest in the stick. | Ignore |
| KS | Juvenile | 26 | e | Observed his mother retrieving the stick from less than 1 m. No interest in the stick. | Ignore |
| KU | Adult | 289 | e | Tries to get the stick out of the hole, succeeds, and plug her hand in the hole, but chased by bees. | Grab |
| KW | Adult | 18 | d | Grab leaf-stick at the same time as her son (KZ). Then takes it to her mouth, smells it, and discards it. | Smell |
| KY | Adult | 71 | d | Takes the leafy-stick out of the hole and discards it without smelling it. | Grab |
| KZ | Adult | 43 | d | Touches leafy-stick at the same time as his mother (KW), but then let go when KW takes it. | Touch |
| MS | Adult | 109 | a, b, c | a: takes stick out without smelling it. b: takes leafy-stick out, inspects and smells combs. c: takes leafy-stick out, smells and licks the leaves. | Lick |
| NB | Adult | 437 | a, b | a: takes leafy-stick out of the hole and discards it without smelling it the first time. Second time, licks the stick before discarding it. b: Ignores the leafy-stick. | Lick |
| NK | Adult | 12 | e | Does not show any interest in the leafy-stick. | Ignore |
| NT | Juvenile | 887 | a, b | a, b: never pays attention to the leafy-stick in the hole that her mother (NB) retrieves. Proceeds to manufacture a leaf-sponge and acquires honey. | Ignore |
| OK | Adult | 42 | e | Retrieves and smells leafy-stick but discards it. | Smell |
| RE | Sub-Adult | 8 | a | Ignores leafy-stick in the hole. | Ignore |
| SQ | Adult | 202 | a, b | a: takes the leafy-stick out of the hole, but discards it without smelling it. b: pays attention to the combs but discards the leafy-stick once the combs are retrieved. | Smell |
| ZK | Juvenile | 114 | e | Appears confused by the task. Touches the leafy-stick but never retrieves it. | Touch |
| ZL | Adult | 73 | d, e | d: Touches the leafy-stick but does not retrieve it. e: retrieves and smells the leafy-stick, but discards it. | Smell |

'Action' represents the highest level of engagement with the experimental tool by the individuals, ranked on an ordinal scale as Ignore, Touch, Grab, Smell, Lick, and Use. No individual ever used the stick to access the honey. Pink: Leaf-spongers.

## 4. Discussion

### Emulation is insufficient for chimpanzees to learn tool use

These results do not support the idea that chimpanzees can learn tool use through affordance learning (Tomasello 1996; Tennie et al. 2009), even if the features are made highly conspicuous. Although the exposure was limited, in that each individual was only exposed a few times to the functional properties of the stick, this was done so as to prevent an artificial overexposure to the behaviours (wild chimpanzees are not expected to find a stick inserted into a beehive more than once, if ever). However, the lack of interest of chimpanzees for the stick-part of the tool also suggests that more exposure may not have triggered much more reaction than already obtained here with a good sample size. These results also suggest that wild chimpanzees' physical cognition is less developed than suggested by laboratory work which argued that captive chimpanzees' physical cognition was similar to that of young children (Herrmann et al. 2007). For many scientists who only work in captive settings, emulation is the mechanism occuring when young chimpanzees develop tool use (Tennie et al. 2009). Tennie and colleagues suggest that the presence of the tool next to the place where it is being used by other individuals is enough to trigger an individual to develop the behaviour. However, my results are in opposition to this hypothesis. If this were the case, given that I exposed both communities with the same tool, its affordances should have been the same for all individuals, irrelevantly of their community of origin. However, my study suggests that using sticks or leaf-sponges as tools to extract resources apparently produces profound changes in the cognition of wild chimpanzees, such that different aspects of their environment become salient to them, regardless of presentation. Kanyawara stick-users found the stick-part of the tool most useful, while Sonso leaf-spongers discarded it in favour of the leaves, suggesting a cultural bias in how they comprehended the new proposed tool.

All the same, these results are not necessarily incompatible with the ones found in captivity. For instance, the results of this study are in line with research on sanctuary chimpanzees, which has demonstrated that individuals rely on previously acquired foraging techniques, with no evidence for modifications to improve efficiency, a phenomenon named 'conservatism' (Marshall-Pescini and Whiten 2008; Hrubesch et al. 2009). In chapter 4, I have shown that wild chimpanzees rely heavily on previously acquired knowledge to solve new problems. The data provided in this chapter show that this knowledge also restricts them

from finding insightful solutions to a novel problem, in that they will keep on using what they know rather than experimenting with new uncertain techniques. Relying on such knowledge to master one's environment rather than experimenting with new techniques individually on an ad-hoc basis may be more adaptive to cope with chimpanzees' competitive and challenging natural environment (Boyd and Richerson 1996; Laland 2001). Although this finding is clearly linked to chimpanzee conservatism, I think that these results suggest a deeper cause to their cognitive blockage. In the former studies (Marshall-Pescini and Whiten 2008; Hrubesch et al. 2009), chimpanzees had learnt a technique that allowed them to get some reward and failed to switch to a technique that was more rewarding. However, most of the Sonso chimpanzees who engaged in the second experiment had still not found a solution to obtain honey. Even when given clues to the solution, they still failed to understand and apply this new technique. While conservatism occurs when individuals stick to a successful technique, it should not occur when they have not learned any technique and thus remain unsuccessful.

Altogether, these results suggest that emulative learning is probably not enough for chimpanzees to develop tool use. The presence of the same tool that was used by a stick-using community to fish for honey was considered irrelevant by most chimpanzees in a non stick-using community, who at best found another part of it salient in relation to their own cultural preferences. These results also suggest that the presence of an experienced model may be crucial for the acquisition of the tool use behaviours (Matsuzawa et al. 2001). Future work is needed to address the interaction between the various social influences to which individuals are exposed to on a daily basis, and the individual learning processes that may be necessary in learning new techniques (Whiten et al. 2004).

**The cognitive dimension of chimpanzee culture**

The major problem with the concept of emulation (*sensu* Tomasello 1996) is that it assumes a highly developed chimpanzee cognition. The assumption is that a naïve individual acquires a new technique by understanding the causal relationship between means and ends, regardless of it is being presented by another individual or a physical reaction of the environment. Additionally, it expects all chimpanzees to conform to a certain ideal of a 'blank slate' chimpanzee that could learn anything as far as the right conditions are present, without taking into account the ontogeny of the individual and the different stimuli it has been exposed to

during its development. In contrast, my results are consistent with the notion of a ‘cultural bias’, which constrains how chimpanzees perceive and evaluate their environment. Individuals acquire their knowledge of tool use in a socially-structured environment but with trial-and-error learning most likely playing a key role (Matsuzawa et al. 2001; Fragaszy and Visalberghi 2004), consistent with a 'hybrid-learning' framework (Sterelny 2006). In some ways, it does not matter what sorts of social learning processes have been at work to build the community-specific pattern of habits that subjects rely on to solve the task (de Waal and Bonnie 2009). Although habits can be acquired individually (Pesendorfer et al. 2009), in chimpanzees this takes place within a social framework, giving each community its unique pattern and fulfilling therefore one of the main requirements of current definitions of animal culture (Quiatt and Reynolds 1993). It is possible that the Sonso individuals simply did not see the point of using the ‘leafy stick’ as a stick because in their social environment, sticks are never used during food acquisition, and thus, they did not make this crucial connection during the second experiment, even when extracting the tool by themselves. The circumstances in which social learning occurs in wild chimpanzees are poorly researched, though there is evidence that complicated procedures, such as termite fishing or stone tool use, are partly acquired from observing mothers and experienced individuals (Matsuzawa et al. 2001; Biro et al. 2003; Lonsdorf et al. 2004; Lonsdorf 2005). Both Sonso and Kanyawara infants grow up in a world of leaves, twigs and branches, and both spend significant amounts of time playing with these objects. Moreover, the same genera of honeybees from which chimpanzees acquire honey are found in both forests, so that the ecological affordances of natural bee hives should be the same. Nevertheless, as adults, Kanyawara individuals reliably develop habitual stick use during food acquisition while Sonso individuals rarely manipulate sticks throughout their lives.

Given that infant chimpanzees at Sonso play with sticks but that adults barely pay attention to them to the point of not considering them as potential material to succeed in a task, an ontogenetic influence is probably at the origin of this loss of interest for sticks, which is not observed in Kanyawara. Since sticks are not used in Sonso for food acquisition, grooming, resting or travelling, the main diurnal activities of wild chimpanzees (Goodall 1986), nor in sexual interactions, they may generally be judged as irrelevant objects, a phenomenon that can have powerful inhibitory effects on learning (cf the 'learned irrelevance' effect, Mackintosh 1974). The fact that different functions of the same tool are perceived by members of the two communities may thus be the product of different childhoods.

This cultural bias may result from a cultural override (Haun et al. 2006b) in chimpanzee cognition, in that some parts of the environment can lose their attraction and become totally irrelevant to developing chimpanzees because their mother and other experienced individuals do not show any interest in them. Future research needs to address how exposure to a mother's actions during infancy shapes the way chimpanzees see the world, and how this determines which aspects they will perceive as salient in adulthood. This study also suggests that definitions of animal culture based on behavioural patterns alone neglect the richness of the phenomenon (Hill 2009). Instead, at least in the case of chimpanzees, there seems to be a profound cognitive dimension to socially acquired behaviours, suggesting that chimpanzee culture is also a manifestation of underlying cognitive differences (Whiten et al. 2003; Whiten 2011). Whether such differences should be interpreted as 'socially imprinted shared set of ideas', a definition of culture that would be accepted by most researchers of human cultural behaviour (Richerson and Boyd 2005; Hill 2009), will have to be resolved by future research.

# Chapter six: Why don't chimpanzees in Budongo use sticks?

Results from this study have been submitted for publication in:

**Gruber, T.,** Krupenye, C., Byrne, M.-R., Mackworth-Young, C. McGrew, W.C., Reynolds, V. & Zuberbühler, K. The influence of ecology on chimpanzee cultural behaviour: A case study of five Ugandan chimpanzee communities. *Submitted*.

## Summary

The influence of ecology on the development of behavioural traditions in animals is controversial. This is particularly true for chimpanzees, where it has been difficult to rule out environmental influences as a cause for the widely observed community-specific behavioural differences. In this chapter, I address this issue by reviewing data from behavioural ecological studies and field experiments from different chimpanzee communities in Budongo and Kibale forests. Specifically, I compare food quality and dietary preferences of five populations, their tool sets, and examine the presence of a particular behaviour, fluid-dip, in four communities with the standardised honey-trap experiment. My results show that although environment, and as a consequence chimpanzee diet, can vary drastically between very close communities, current differences in ecology are poor predictors of behavioural traditions. Rather, it is more likely that the ecology constitutes a force, which can contribute to innovation or loss of behavioural traditions while their maintenance is better explained with social factors. Using information on the recent evolutionary history of the Ugandan forests and chimpanzees, I discuss the potential impact of ecological, genetic and socio-cognitive factors on behavioural innovations and extinctions leading to chimpanzee cultures.

## 1. Introduction

Chimpanzees are some of the most accomplished tool-users in the animal kingdom, a finding that has implications for understanding the evolutionary origins of human cognition and capacity for culture. However, it has also long been known that wild chimpanzee communities vary in their use of tools and, notably, that some communities have more tool variants than others (McGrew 1992; Whiten et al. 1999; McGrew 2010). As already mentioned in the preceding chapters, an ongoing source of contention concerns the nature of the mechanisms that have led to the observed behavioural diversity and whether it qualifies as culture. One pertinent line of reasoning is that the ecological or genetic differences between the different communities are so minimal that, by default, any observed behavioural differences must be 'cultural' (de Waal 1999). However, others have argued that the habitats of wild chimpanzees are too complex to rule out ecological explanations a priori or without specific empirical data (Galef 1992; Tomasello 1999). It has also been argued that group-specific behavioural differences will always be a product of interactions between ecological, genetic and social factors (Laland and Janik 2006; Krützen et al. 2007; Laland and Janik 2007), a stance also adopted by recent field studies (Möbius et al. 2008; Schöning et al. 2008). In chapters 4 and 5, I have experimentally shown that at least one specific behaviour, fluid-dip, was absent in the Sonso community of Budongo Forest, while it is present in the Kanyawara community of Kibale National Park, less than 200 km away. In these chapters, I have argued that these results can be explained as cultural differences, notably because the observed variation is not only at the behavioural but also at the cognitive level. Yet, it has not been possible to rule out that genetic or subtle ecological differences between the two populations are the main causes of the observed variation. In this chapter, therefore, I aim to address the origin of this variation by comparing genetic, ecological and behavioural data available for the different communities. The following three scenarios seem likely: 'local adaptation', 'ontogenetic flexibility', and 'cultural difference' (van Schaik et al. 2009a).

Under the first scenario, local adaptation, the observed differences in 'fluid-dip' could be due to genetic differences between the two groups that are sufficient to provoke this subtle behavioural difference. To test this hypothesis, I analysed two sets of data. First, I carried out experimental work with two other communities in the Budongo forest, the Busingiro and Kaniyo Pabidi communities, to explore if the Sonso chimpanzees were somehow unusual.

Subsequently, I added the Ngogo community of Kibale forest to the analysis because some individuals of this group are known to use sticks during food acquisition (Watts 2008). Second, I compared the tool catalogues of the Ugandan and Tanzanian communities. All belong to the same subspecies but Ugandan communities appear to differ in their feeding-related tool-using behaviours (McGrew 2010). Therefore I wanted to investigate whether Ugandan communities were generally limited in terms of their tool-using abilities. If clear behavioural differences in tool use were to be found between these two sets of communities, then it could indicate a genetic difference. However, if the two sets of communities had similar tool-using behaviours, this would make this hypothesis unlikely.

According to the second scenario, ontogenetic flexibility, ecological differences are the main cause for behavioural differences between sites: individuals develop behavioural differences in response to particular ecological conditions, independently of each other (Tennie et al. 2009). To test this hypothesis, I conducted a broad analysis of the ecology of the Sonso, Kanyawara and Ngogo communities. For these three communities, data have already been collected and published with comparable methods (Sonso: Newton-Fisher (1999b); Fawcett (2000); Tweheyo et al. (2004); Kanyawara: Wrangham et al. (1991; 1993; 1996); Ngogo: Potts et al. (in press)). I compared these records and complemented them with new data from the two other communities at Kaniyo Pabidi and Busingiro. I subsequently put these differences in relation to the tool-using variations to analyse if the current ecological variation could be responsible for the presence or absence of fluid-dip.

The third scenario, cultural diversity, has already been addressed in chapters 4 and 5. To assess the plausibility of this scenario, I put the behavioural data collected in Budongo and Kibale forests in relation with the recent ecological history of these forests. During the Pleistocene, tropical forests in Africa experienced periods of expansion and contraction due to climatic changes (Kendall 1969; van Zinderen Bakker and Coetzee 1972; Moeyersons and Roche 1982). The last expansion of Sub-Saharan forests is thought to have peaked around 12,500 years ago (Hamilton 1976; Haffer 1982; Mayr and O'Hara 1986; Hamilton 1988). At this time, Budongo and Kibale were part of a continuous forest, which had originated from a core area in north-eastern DR Congo (Hamilton 1976; Grubb 1982; Howard 1991). Since then, the forests have generally retracted, in recent times mainly due to anthropogenic activities (Philipson 1977; Hamilton 1984; Hamilton et al. 1986; Howard 1991). It is estimated that the western forests, including Budongo and Kibale, became separated from one another between 8,000 and 10,000 years ago (Reynolds 2005). Although the evolutionary

history of the forests and their chimpanzee communities are closely related, an unusual pattern is thought to have occurred for the Great Rift region of East Africa. The genetic diversity of Eastern African chimpanzees is low, suggesting that they are the descendants of a small population of no more than 6,000 individuals (Goldberg 1996). During the last Ice Age, rather than retracting into forested refugia, this population is thought to have occupied woodland habitats during arid, colder and less forested episodes, which may have kept their population size low (Goldberg 1996; Goldberg and Ruvolo 1997a, b). If this third scenario is accurate, the small original gene pool suggests that the observed behavioural differences are less likely to have genetic causes and that social processes may provide a better explanation.

## 2. Methods

### Experimental tool tests

I tested members of the Kaniyo Pabidi and Busingiro community for their tool-using skills by exposing them to a honey-trap apparatus that I previously used at Sonso and Kanyawara (see chapters 2, 4 and 5). In brief, the apparatus consisted of a 25 cm wide wood log of a standardised length of 50 cm with an artificial hole with a 5x4 cm opening and 16 cm depth. I prepared several such logs, which I then positioned at places where the chimpanzees were likely to visit. The hole was filled with honey up to 10 cm below the surface every morning before the chimpanzees arrived. Honeycombs were used to cover the hole to protect it from insect invasion and to provide a visual cue for the chimpanzees. At both sites, I was helped by research assistants (Busingiro: C.K.; Kaniyo Pabidi: M.R.B. and C.M.Y.).

At Busingiro, a motion-sensitive video camera (PixController DVREye) was positioned to survey the apparatus and a surrounding area of about 20 $m^2$. At Kaniyo Pabidi, video recordings were made directly by the observers with a Canon FS100 camcorder. As a tool, I provided a 40 cm long branch of an *Alstonia sp.* stripped of all leaves over half of its length, the 'leafy stick'. At both sites, I exposed individuals to the following experimental conditions: (a) no tool, (b) tool next to the hole and (c) tool inside the hole. Tourism activity and poor habituation complicated systematic data collection at both sites so that the conditions could not be compared systematically.

**Comparison of tool catalogues between sites**

I compared the tool catalogues of the Ugandan populations with records from other long-term study groups of the same subspecies (Mahale-M, Mahale-K and Gombe, all in Tanzania; data extracted from Whiten et al. 1999) to examine if there were particular differences between food related and non-food related tool use between them. After ensuring that the data were normally distributed, I conducted One-Way ANOVAs with the number of tool behaviours in each case as variables and the population (Ugandan or Tanzanian) as the determining factor. I could not use data on food diversity and extractive tool-using behaviours from the Sonso, Kanyawara and Ngogo communities because of small sample size. I provide a qualitative comparison of the three communities.

**Habitat ecology and dietary preferences**

To describe the different habitats, I compared data published by Chapman et al. (1999) for the Kanyawara and Ngogo communities with data published by Plumptre and Reynolds (1994), resulting from a 1992 survey of the Budongo Forest as these two studies used comparable methods to sample the composition of the forests (the authors recorded all trees with a diameter at breast height (DBH) > 10 cm) over comparable areas (Sonso: 3.3 ha; Kanyawara: 2.4 ha; Ngogo: 4.8 ha). By putting all the tree species together, I generated a database where I calculated the density of each tree species at each site. This allowed me to compare the three sites in terms of their tree composition (with d = 0.0 meaning that the given species was absent from the site, Table 6.2). I also used the data published in Plumptre et al. (1997) to include the overall composition of Budongo Forest in the general comparison. I used Pearson Chi-Square tests to compare the proportion of edible and non-edible trees in the home range of the three study groups (Sonso, Ngogo and Kanyawara).

A widely used quantitative method to describe dietary diversity is the Shannon-Wiener Index ($H' = - \sum [Pi.lnPi]$, where Pi is the proportion of the species 'i' in the overall diet). Diversity is calculated by relating each consumed food type to its frequency of use over a given time period. Larger H' values indicate greater diversity. A related measure is the Standardised Shannon-Wiener Diversity Index (J'), or Hill's Equality Index (Hill 1973), which is defined as $J' = H'/\ln(x)$, with x being the total number of food types included in the diet during the sampling period. J' therefore is a score between 0 and 1, with 1 indicating maximum

equitability of feeding time among all food types. I calculated the average monthly Shannon-Wiener Diversity indices for all three groups using data published by Potts (in press) and Newton-Fisher (1999b) and compared them using independent T-tests. Although the years when the studies were conducted differed, I controlled for seasonality by comparing overlapping months (e.g., January-June or June-December periods at both sites) assuming that seasonal patterns had remained largely similar over time. I used Pearson Chi-Square to compare the different diet components (e.g., ripe fruits, flowers) of the three communities. For Busingiro and Kaniyo Pabidi, such data were not available. Thus, I used faecal sample data provided by Plumptre et al. (1997) to estimate chimpanzee dietary preferences. Additionally, for Kaniyo Pabidi, I analysed N = 1,205 feeding records, collected by six local field assistants between December 3rd, 2006 and September 4th, 2010 during daily trackings. As species names were not always given, I analysed the data at the genus level.

## 3. Results

### 3.1. Assessment of the 'local adaptation' hypothesis

#### Experimental investigation of fluid-dip in Kaniyo Pabidi and Busingiro

I carried out the honey-trap experiment with members of the Kaniyo Pabidi and Busingiro communities to assess the presence of the fluid-dip behaviour. Five individuals were tested at Kaniyo Pabidi on 9 different occasions and on 7 different days in both the 'no tool' and 'tool inside the hole' conditions. They engaged with the hole for a total of 18 minutes and 9 seconds. Responses were very similar to the Sonso chimpanzees, with no instance of use of the provisioned tool, the leafy stick, as a stick or a brush. In contrast to Sonso, however, no individual was seen leaf-sponging. Instead, all individuals used their hands to try to access honey. At Busingiro, at least 10 different individuals were tested over seven days (1 followed by 6 in a row). Individuals engaged with the hole for a total of 30 minutes and 22 seconds but reliable identification of individuals was not possible, as the community was not habituated at the time of the study. No individual used the provided tool or any other tool to try to retrieve honey.

**Comparison of tool catalogues between Ugandan and Tanzanian communities**

Comparing the three Ugandan communities with three other *P. t. schweinfurthii* groups (Mahale-M, Mahale-K and Gombe, all three in Tanzania), I found that the Ugandan communities showed significantly less tool-using behaviours during food extraction than the other communities (One-Way ANOVA, df = 1, F = 9.846, p = 0.035). However, I found no difference in tool-using behaviour in non-food related activities, if they were considered together (One-Way ANOVA, df = 1, F = 0.018, p = 0.900, Table 6.1). Additionally, in Sonso only 1 of 11 tool-using behaviours was for extractive purposes; in Kanyawara it was 2 of 11, and in Ngogo 4 of 11. Although the three communities all used leaves to extract water from holes, only the chimpanzees of Kanyawara and Ngogo used sticks to extract honey from beehives. Additionally, Ngogo individuals made more use of sticks by using them to enlarge holes and they were observed to fish for insects with twigs. Although, in theory, the Ngogo chimpanzees' extractive tool set could be compared to the Mahale-M community, stem wand has only been observed very rarely in Ngogo (Watts 2008) while the equivalent fishing behaviours are customary at Mahale. Thus, the Ngogo chimpanzees are also limited in their extractive use of tools. In any case, Sonso and Kanyawara are the communities with the smallest tool-using diversity during food extraction of all communities (Table 6.1).

**Table 6.1.** Comparison of tool-using behaviours in 3 Tanzanian (Gombe, Mahale-M and Mahale-K) and 3 Ugandan (Kanyawara, Sonso, Ngogo) *Pan troglodytes schweinfurthii* communities as described in Watts, 2008 and Whiten et al. 1999.

| Context | Watts (2008) | Whiten et al. (1999) | Gombe | Mahale M | Mahale K | Kanyawara | Sonso | Ngogo |
|---|---|---|---|---|---|---|---|---|
| Food Extraction | Leaf-sponge | Leaf-sponge | 1 | 1 | | 1 | 1 | 1 |
| | Stick probe | Fluid-dip | 1 | 1 | 1 | 1 | | 1 |
| | Stick lever | Lever open | 1 | | | | | 1 |
| | Stem wand | Termite-fish | 1 | | 1 | | | 1 |
| | | Termite-fish leaf | | | 1 | | | |
| | | Expel/stir | 1 | 1 | 1 | | | |
| | | Bee-probe | | | 1 | | | |
| | | Ant-dip-single | 1 | | | | | |
| | | Ant-dip-wipe | 1 | 1 | 1 | | | |
| | | Ant-fish | 1 | 1 | 1 | | | |
| | | Leaves-mop | 1 | | 1 | | | |
| | | Leaf-wipe | 1 | | | | | |
| TOTAL | | | 10 | 5 | 8 | 2 | 1 | 4 |
| Hygiene | Leaf napkin | Leaf-napkin | 1 | 1 | | 1 | 1 | 1 |
| | | Leaf-dab | 1 | | | 1 | 1 | 1 |
| | | | | | | | | |
| Comfort | Bee whisk | Fly-whisk | 1 | | | | 1 | 1 |
| | | Leaf-brush | 1 | | | | | |
| | | Comb | | | | | 1 | |
| | | | | | | | | |
| Aggression | Club | Club | 1 | 1 | | 1 | | 1 |
| | Missile | Aimed-throw | 1 | 1 | | 1 | 1 | 1 |
| | | Drag branch | 1 | 1 | 1 | 1 | 1 | |
| | | | | | | | | |
| Attract attention | Leaf-clip | Leaf-clip (mouth) | | 1 | 1 | 1 | 1 | 1 |
| | Branch-wave | Branch-shake | 1 | 1 | 1 | 1 | 1 | 1 |
| | | Leaf-strip | 1 | 1 | | 1 | | |
| | | | | | | | | |
| Other | | Leaf-inspect | 1 | | | | 1 | |
| | | Investigatory probe | 1 | 1 | 1 | 1 | 1 | |
| | | Container | 1 | | | | | |
| | | Nasal probe | | 1 | | | | |
| TOTAL | | | 12 | 9 | 4 | 9 | 10 | 7 |

'1': This code does not take into account frequency of use, only that the behaviour has been observed in the community.

### 3.2. Assessment of the 'ontogenetic flexibility' hypothesis

#### Comparative ecology of Budongo and Kibale Forests

A total of 148 tree species were described in previous studies throughout the home range of the three main study groups at Sonso, Kanyawara and Ngogo (Plumptre et al. 1997; Chapman et al. 1999). At Sonso, 95 tree species were identified; 45.2% of which were eaten by chimpanzees. At Kanyawara and Ngogo, 61 and 59 species were identified, respectively, with 26.2% and 25.9% of them eaten (Table 6.2). In pairwise comparisons, I found that 44/148 (29.7 %) trees differed between Kanyawara and Ngogo, with 10/44 being edible. The difference between Sonso and Kanyawara was 41/108 (38.0 %), similar to the difference between Sonso and Ngogo, 39/106 (36.8 %) ($\chi^2_1 = 0.031$, $p = 0.86$).

If a larger and more representative section of Budongo Forest was considered, including 6 different sites (1992 census: Plumptre et al. 1997), I found that of all 148 species, only 18 were absent throughout Budongo Forest, 2/18 (11.1%) of which were eaten by chimpanzees. At Sonso, 53 of 148 species (35.8%) were absent; nine of which (17.0%) were eaten by chimpanzees. In comparison, at Kanyawara 87 of 148 (58.8%) were missing, 36 of which (41.4%) were eaten by chimpanzees, while at Ngogo 67 of 148 (45.3%) were missing, 30 of which (44.8%) were eaten by chimpanzees. Thus, by all accounts, Budongo Forest represents an extremely diverse habitat for chimpanzees, with most edible and inedible trees of both forests represented, while Kibale Forest offers a much more restricted range of tree species suitable as chimpanzee foods.

**Table 6.2.** Ecological composition and comparison of differences between Budongo and Kibale forests at the Sonso (S), Ngogo (N) and Kanyawara (K) sites.

| | | Density (individuals.ha$^{-1}$) | | | Species absent in (1 = species is absent) | | | | | Pairwise comparison (1 = different) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | Edible | S | K | N | Bud | Kib | S | K | N | # S-K | # S-N | # N-K |
| *Acacia spp.* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Albizia grandibracteata* | Non Edible | 2.4 | 1.3 | 0.0 | | | | | 1 | | 1 | 1 |
| *Alchornea laxiflora* | Non Edible | 6.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Allophylus dummeri* | Non Edible | 0.9 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Alstonia boonei* | Edible | 9.9 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Aningeria altissima* | Non Edible | 0.3 | 1.7 | 0.0 | | | | | 1 | | 1 | 1 |
| *Antiaris toxicaria* | Edible | 5.1 | 0.4 | 0.0 | | | | | 1 | | 1 | 1 |
| *Antidesma laciniatum* | Non Edible | 2.7 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Aphania senegalensis* | Non Edible | 0.0 | 1.7 | 4.6 | | | 1 | | | 1 | 1 | |
| *Apodytes dimidiata* | Non Edible | 5.1 | 0.8 | 0.0 | | | | | 1 | | 1 | 1 |
| *Argomuellera macrophylla* | Non Edible | 1.2 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Balanites wilsoniana* | Non Edible | 0.0 | 1.7 | 1.7 | | | 1 | | | 1 | 1 | |
| *Beilshmiedia ugandensis* | Non Edible | 0.0 | 0.4 | 0.0 | 1 | | 1 | | 1 | 1 | | 1 |
| *Belonophora hypoglauca* | Non Edible | 2.1 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Bersama abyssinica* | Non Edible | 0.0 | 0.4 | 0.0 | | | 1 | | 1 | 1 | | 1 |
| *Blighia sp.* | Non Edible | 1.5 | 0.8 | 1.0 | | | | | | | | |
| *Bosqueia phoberos* | Non Edible | 3.3 | 50.0 | 5.6 | | | | | | | | |
| *Bridelia micrantha* | Non Edible | 1.2 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Broussonetia papyrifera* | Edible | 3.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Caloncoba schweinfurthii* | Edible | 6.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Casearia sp.* | Non Edible | 0.0 | 1.3 | 0.2 | 1 | | 1 | | | 1 | 1 | |
| *Cassine buchananii* | Edible | 0.0 | 0.4 | 2.7 | 1 | | 1 | | | 1 | 1 | |
| *Cassipourea ruwensorensis* | Non Edible | 0.0 | 7.1 | 5.0 | 1 | | 1 | | | 1 | 1 | |
| *Celtis africana* | Non Edible | 0.0 | 4.2 | 1.0 | | | 1 | | | 1 | 1 | |
| *Celtis durandii* | Edible | 34.7 | 47.1 | 57.5 | | | | | | | | |
| *Celtis wightii/philippensis* | Edible | 1.8 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |

| (continued) | | Density (individuals.ha$^{-1}$) | | | Species absent in (1 = species is absent) | | | | | Pairwise comparison (1 = different) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | Edible | S | K | N | Bud | Kib | S | K | N | # S-K | # S-N | # N-K |
| *Chaetacme aristata* | Non Edible | 0.3 | 17.1 | 4.8 | | | | | | | | |
| *Chrysophyllum sp.* | Edible | 8.4 | 2.6 | 64.6 | | | | | | | | |
| *Cleistopholis patens* | Edible | 2.1 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Coffea eugenoides* | Non Edible | 0.0 | 0.4 | 0.0 | | | 1 | | 1 | 1 | | 1 |
| *Cola gigantean* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Cordia africana* | Non Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Cordia millenii* | Edible | 4.8 | 0.4 | 0.2 | | | | | | | | |
| *Craterispermum laurinum* | Non Edible | 0.0 | 1.7 | 0.0 | 1 | | 1 | | 1 | 1 | | 1 |
| *Crossonephelis africanus* | Non Edible | 0.9 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Croton sp.* | Edible | 13.5 | 0.8 | 0.4 | | | | | | | | |
| *Cynometra Alexandrii* | Edible | 13.2 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Dasylepis sp.* | Non Edible | 0.0 | 1.3 | 7.9 | | | 1 | | | 1 | 1 | |
| *Desplatsia dewevrei* | Edible | 3.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Dictyandra arborescens* | Non Edible | 0.0 | 0.4 | 12.1 | | | 1 | | | 1 | 1 | |
| *Diospyros abyssinica* | Non Edible | 3.3 | 40.0 | 69.0 | | | | | | | | |
| *Dombeya kirkii* | Non Edible | 0.0 | 9.2 | 3.1 | | | 1 | | | 1 | 1 | |
| *Dovyalis macrocalyx* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Drypetes ugandensis* | Non Edible | 1.8 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Entandrophragama cylindricum* | Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Entandrophragama utile* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Entandrophragma angolense* | Edible | 0.3 | 0.0 | 0.2 | | | | 1 | | 1 | | 1 |
| *Erythrina abyssinica* | Non Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Erythrophleum suaveolens* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Euadenia eminens* | Non Edible | 0.0 | 0.0 | 0.2 | | | 1 | 1 | | | 1 | 1 |
| *Euclinia longiflora* | Non Edible | 0.0 | 0.8 | 0.0 | 1 | | 1 | | 1 | 1 | | 1 |
| *Fagara lepriurii (Zanthoxyllum lepriurii)* | Non Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Fagaropsis angolensis* | Non Edible | 0.6 | 2.5 | 0.6 | | | | | | | | |
| *Ficus cyathistipula* | Edible | 0.0 | 0.0 | 1.0 | 1 | | 1 | 1 | | | 1 | 1 |
| *Ficus exasperata* | Edible | 0.6 | 3.8 | 0.4 | | | | | | | | |
| *Ficus lingua* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |

| (continued) | | Density (individuals.ha$^{-1}$) | | | Species absent in (1 = species is absent) | | | | | Pairwise comparison (1 = different) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | Edible | S | K | N | Bud | Kib | S | K | N | # S-K | # S-N | # N-K |
| *Ficus natalensis* | Edible | 0.0 | 0.4 | 0.6 | | | 1 | | | 1 | 1 | |
| *Ficus ovate* | Non Edible | 0.0 | 0.0 | 0.2 | 1 | | 1 | 1 | | | 1 | 1 |
| *Ficus sansibarica* | Edible | 0.0 | 1.7 | 2.1 | | | 1 | | | 1 | 1 | |
| *Ficus saussureana* | Edible | 0.3 | 0.0 | 0.6 | | | | 1 | | 1 | | 1 |
| *Ficus sur* | Edible | 6.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Ficus trichopoda* | Non Edible | 0.3 | 0.0 | 0.4 | | | | 1 | | 1 | | 1 |
| *Ficus variifolia* | Edible | 4.2 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Funtumia latifolia* | Non Edible | 69.8 | 33.8 | 36.3 | | | | | | | | |
| *Glyphaea brevis* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Guarea cedrata* | Non Edible | 3.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Harrisonia abyssinica* | Non Edible | 0.0 | 0.0 | 2.5 | 1 | | 1 | 1 | | | 1 | 1 |
| *Harungana madagascariensis* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Holoptelea grandis* | Non Edible | 1.5 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Khaya anthoteca* | Edible | 15.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Kigelia moosa* | Non Edible | 0.3 | 3.3 | 0.8 | | | | | | | | |
| *Lasiodiscus mildbraedii* | Edible | 31.7 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Leptaulus daphnoides* | Non Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Leptonychia mildbraedii* | Non Edible | 0.0 | 35.4 | 2.5 | | | 1 | | | 1 | 1 | |
| *Lindackeria sp.* | Non Edible | 0.0 | 0.0 | 1.3 | | | 1 | 1 | | | 1 | 1 |
| *Linociera johnsonii* | Non Edible | 0.3 | 5.4 | 7.5 | | | | | | | | |
| *Lovoa swynnertonii* | Non Edible | 0.0 | 0.8 | 4.4 | | | 1 | | | 1 | 1 | |
| *Lovoa trichilioides* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Lychnodiscus cerospermus* | Non Edible | 3.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Macaranga scheiwinfurthii* | Edible | 0.3 | 0.0 | 0.4 | | | | 1 | | 1 | | 1 |
| *Maerua duchesnei* | Non Edible | 0.0 | 1.3 | 0.4 | | | 1 | | | 1 | 1 | |
| *Maesopsis eminii* | Edible | 10.8 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Majidea fosteri* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Mammea africana* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Markhamia lutea* | Non Edible | 0.3 | 50.0 | 24.8 | | | | | | | | |
| *Milicia (Chlorophora) excels* | Edible | 1.8 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |

| (continued) | | Density (individuals.ha$^{-1}$) | | | Species absent in (1 = species is absent) | | | | | Pairwise comparison (1 = different) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | Edible | S | K | N | Bud | Kib | S | K | N | # S-K | # S-N | # N-K |
| *Mimusops bagshawei* | Edible | 0.0 | 3.3 | 3.1 | | | 1 | | | 1 | 1 | |
| *Mitragyna rubrostipulata* | Non Edible | 1.2 | 0.0 | 0.4 | | | | 1 | | 1 | | 1 |
| *Monodora angolensis* | Edible | 0.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Monodora myristica* | Edible | 0.0 | 0.4 | 0.4 | | | 1 | | | 1 | 1 | |
| *Morus lacteal* | Edible | 1.5 | 0.0 | 0.2 | | | | 1 | | 1 | | 1 |
| *Myrianthus arboreus* | Edible | 5.7 | 2.1 | 0.0 | | | | | 1 | | 1 | 1 |
| *Neoboutonia sp.* | Non Edible | 1.5 | 1.3 | 7.9 | | | | | | | | |
| *Newtonia buchananii* | Non Edible | 0.0 | 0.0 | 0.2 | | | 1 | 1 | | | 1 | 1 |
| *Olea capensis* | Non Edible | 0.6 | 3.3 | 3.1 | | | | | | | | |
| *Oncoba sp.* | Non Edible | 0.3 | 0.0 | 0.4 | | | | 1 | | 1 | | 1 |
| *Oxyanthus latifolia* | Non Edible | 0.0 | 0.0 | 0.4 | | | 1 | 1 | | | 1 | 1 |
| *Pancovia turbinata* | Non Edible | 0.0 | 10.8 | 0.2 | | | 1 | | | 1 | 1 | |
| *Parinari excelsa* | Non Edible | 0.0 | 2.9 | 0.2 | | | 1 | | | 1 | 1 | |
| *Parkia filicoidea* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Paropsia guineensis* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Picralima nitida ('quinine')* | Edible | 1.2 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Piptadeniastrum africanum* | Non Edible | 0.0 | 0.0 | 1.9 | | | 1 | 1 | | | 1 | 1 |
| *Pleiocarpa pycnantha* | Non Edible | 0.0 | 1.3 | 1.3 | 1 | | 1 | | | 1 | 1 | |
| *Polyscias fulva* | Non Edible | 0.0 | 0.8 | 0.2 | 1 | | 1 | | | 1 | 1 | |
| *Premna angolensis* | Non Edible | 0.0 | 4.6 | 4.4 | | | 1 | | | 1 | 1 | |
| *Prunus africana* | Non Edible | 0.0 | 0.0 | 3.0 | | | 1 | 1 | | | 1 | 1 |
| *Pseudospondias microcarpa* | Edible | 0.9 | 1.7 | 1.3 | | | | | | | | |
| *Psidium guajava* | Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Psychotria sp.* | Non Edible | 0.0 | 0.0 | 0.2 | 1 | | 1 | 1 | | | 1 | 1 |
| *Pterygota mildbraedii* | Non Edible | 0.0 | 0.0 | 10.8 | | | 1 | 1 | | | 1 | 1 |
| *Raphia farinifera* | Edible | 1.8 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Rauvolfia oxyphylla* | Non Edible | 0.3 | 0.0 | 2.1 | | | | 1 | | 1 | | 1 |
| *Ricinodendron heudelotii* | Edible | 3.6 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Rinorea oblongifolia* | Non Edible | 13.8 | 0.0 | 0.2 | | | | 1 | | 1 | | 1 |

| (continued) | | Density (individuals.ha$^{-1}$) | | | Species absent in (1 = species is absent) | | | | | Pairwise comparison (1 = different) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | Edible | S | K | N | Bud | Kib | S | K | N | # S-K | # S-N | # N-K |
| *Sapium ellipticum* | Non Edible | 0.6 | 0.0 | 0.6 | | | | 1 | | 1 | | 1 |
| *Schrebera arborea* | Non Edible | 0.9 | 0.0 | 1.5 | | | | 1 | | 1 | | 1 |
| *Spathodea campanulata* | Non Edible | 0.0 | 0.8 | 2.3 | | | 1 | | | 1 | 1 | |
| *Strombosia scheffleri* | Non Edible | 0.0 | 12.5 | 3.1 | 1 | | 1 | | | 1 | 1 | |
| *Strychnos mitis* | Edible | 0.0 | 7.5 | 0.2 | | | 1 | | | 1 | 1 | |
| *Symphonia globulifera* | Non Edible | 0.0 | 0.4 | 0.0 | | | 1 | | 1 | 1 | | 1 |
| *Tabernaemontana sp.* | Non Edible | 5.7 | 4.6 | 34.4 | | | | | | | | |
| *Tapura fischeri* | Non Edible | 6.9 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Tarenna pavettoides* | Non Edible | 0.0 | 0.0 | 4.4 | 1 | | 1 | 1 | | | 1 | 1 |
| *Teclea nobilis* | Edible | 1.2 | 17.1 | 3.8 | | | | | | | | |
| *Tetrapleura tetraptera* | Non Edible | 3.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Tetrorchidium didymostemon* | Non Edible | 3.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Thecacoris lucida* | Non Edible | 0.0 | 1.3 | 0.0 | 1 | | 1 | | 1 | 1 | | 1 |
| *Treculia africana* | Edible | 0.0 | 0.0 | 0.2 | | | 1 | 1 | | | 1 | 1 |
| *Trichilia dregeana* | Non Edible | 0.3 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Trichilia prieuriana* | Non Edible | 3.0 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Trichilia rubescens* | Edible | 23.9 | 0.0 | 0.0 | | 1 | | 1 | 1 | 1 | 1 | |
| *Turraea sp.* | Non Edible | 0.0 | 0.0 | 1.5 | | | 1 | 1 | | | 1 | 1 |
| *Turraeanthus africanus* | Non Edible | 0.0 | 0.0 | 0.4 | 1 | | 1 | 1 | | | 1 | 1 |
| *Uvariopsis congensis* | Edible | 0.0 | 60.4 | 100.6 | | | 1 | | | 1 | 1 | |
| *Vangueria apiculata* | Non Edible | 0.6 | 0.0 | 0.2 | | | | 1 | | 1 | | 1 |
| *Vitex amboniensis* | Non Edible | 2.1 | 0.0 | 0.2 | | | | 1 | | 1 | | 1 |
| *Warbugia ugandensis* | Non Edible | 0.0 | 0.0 | 1.3 | | | 1 | 1 | | | 1 | 1 |
| *Xymalos monospora* | Non Edible | 0.0 | 8.8 | 2.3 | 1 | | 1 | | | 1 | 1 | |
| *Zanthoxylum leprieurii* | Non Edible | 0.0 | 0.8 | 0.2 | | | 1 | | | 1 | 1 | |
| TOTAL | | | | | 18 | 55 | 53 | 87 | 67 | 108 | 106 | 44 |

**Core diet**

While showing that the ecological composition differs between the three sites, the data described above do not compare if chimpanzee communities actually differ in their diet. Therefore, in the following sections, I compare different aspects of their diet.

Firstly, I compared the most commonly eaten foods at the three sites, so as to compare chimpanzees' favourite foods (Newton-Fisher 1999b; Potts et al. in press). At Ngogo and Kanyawara, a "top 20" list was available: at Kanyawara chimpanzees fed on 13 trees species and 7 species of terrestrial herbaceous vegetation (THV), which accounted for more than 0.95% of feeding time each, or 89.5% total. At Ngogo, the top 20 species consisted of trees only, which accounted for more than 0.7% of feeding time each, or 91.5% total. At Sonso, no top 20 list was available, but the top 17 tree species accounted for more than 0.5% of chimpanzee feeding time each. In addition, the chimpanzees fed on an unspecified number of THV and climber species, which accounted for 3.2% and 1.2% of feeding time, respectively. The 17 trees, climbers and THV accounted for 97.7 % total (Newton-Fisher 1999b). In pairwise comparisons, 8 species were shared between Kanyawara and Ngogo, 5 between Kanyawara and Sonso and 6 between Sonso and Ngogo. Across the three communities, 4 species were common (Table 6.3).

**Table 6.3.** Comparison of preferred trees consumed in Kanyawara, Ngogo and Sonso sorted according to total feeding time spent eating on possibly various parts of a plant.

| Kanyawara | % of feeding time | Ngogo | % of feeding time | Sonso | % of feeding time |
|---|---|---|---|---|---|
| ***Ficus natalensis*** | 17.9 | Ficus mucuso | 34 | ***Ficus capensis*** | 23 |
| ***Ficus sansibarica*** | 16.1 | *Uvariopsis congensis* | 11.1 | Broussonetia papyrifera | 22.7 |
| *Mimusops bagshawei* | 8.3 | Chrysophyllum albidum | 9.8 | Ficus mucuso | 9.8 |
| ***Ficus exasperata*** | 7.62 | Pterygota mildbraedii | 6.97 | Maesopsis eminii | 9.4 |
| Celtis africana | 6.9 | Teclea nobilis | 5.5 | Celtis durandii | 8.4 |
| unk THV * | 5.4 | *Mimusops bagshawei* | 5.1 | Celtis mildbraedii | 4.6 |
| Acanthus arborescens | 5.3 | *Ficus saussureana* | 3.7 | THV* | 3.2 |
| ***Ficus capensis*** | 4.9 | Morus mesozygia | 2.6 | Khaya anthotheca | 2.9 |
| *Uvariopsis congensis* | 3.9 | Pouteria altissima | 2.2 | Croton macrostachys | 2.8 |
| Aframomum spp. | 2.9 | ***Ficus sansibarica*** | 1.7 | ***Ficus exasperata*** | 2.2 |
| Lepistemon spp. | 1.8 | Treculia africana | 1.24 | Cordia millenii | 1.7 |
| Pennisetum purpureum | 1.62 | *Pseudospondias microcarpa* | 1.15 | Climbers | 1.5 |
| *Ficus saussureana* | 1.4 | Cassine buchananii | 1.03 | Desplatsia dewevrei | 1.3 |
| Ensete spp. | 1.27 | Cordia millenii | 0.98 | Cynometra alexandrii | 0.9 |
| Cordia abyssinica | 1.17 | ***Ficus exasperata*** | 0.98 | ***Ficus sansibarica*** | 0.9 |
| *Pseudospondias microcarpa* | 1.14 | ***Ficus natalensis*** | 0.96 | Raphia farinifera | 0.6 |
| Linociera johnsonii | 1.05 | Monodora myristica | 0.95 | ***Ficus natalensis*** | 0.5 |
| Cyperus papyrus | 0.96 | ***Ficus capensis*** | 0.72 | Ficus varifolia | 0.5 |
| | | Cola gigantea | 0.7 | Cleistopholis patens | 0.8 |
| TOTAL | 89.5 | TOTAL | 91.49 | TOTAL | 97.7 |

***bold***: species appearing in the top food of Kanyawara, Ngogo and Sonso. *Italic*: species appearing in the top food of Kanyawara and Ngogo. Underlined: species appearing in the top food of Sonso and Ngogo. *: Common in the top food of Sonso and Kanyawara although the species are not mentioned. Above red line: species accounting for over 50% of total feeding time.

If comparing all foods, rather than only the most preferred ones, I found that the Sonso chimpanzees fed on more than 58 species (15 months study period; Newton-Fisher 1999b). The Kanyawara chimpanzees fed on 58 species (12 months study period; Potts et al. in press). The Ngogo chimpanzees fed on 53 species (12 months study period; Potts et al. in press). In terms of plant items (e.g. leaf, roots), they respectively fed on 118, 64 and 60 different items. At Sonso, fruits (64.5%), leaves (19.7%) and flowers (8.8%) accounted for most of the feeding time. At Kanyawara, fruits (66.5%), THV (17.4%) and leaves (10%) were most common while at Ngogo, the diet was overwhelmingly dominated by fruits (92.2%). The diet composition of the three communities was significantly different ($\chi^2_8 = 50.88$, $p < 0.001$, Table 6.4).

**Table 6.4.** Comparative composition of the diet between the three sites as percentage of feeding time over respectively a 15-month period (Sonso; Newton-Fisher, 1999) and a 12-month period (Kanyawara and Ngogo; Potts, in Press).

| Type of food | Kanyawara | Ngogo | Sonso |
|---|---|---|---|
| Ripe Fruits | 64.6 | 80.5 | 54.6 |
| Unripe Fruits | 2.0 | 11.0 | 9.9 |
| Flowers | *inc. in others* | *inc. in others* | 8.8 |
| Leaves | 11.4 | 3.5 | 19.7 |
| THV | 17.4 | 1.1 | 3.2 |
| Others | 4.6 | 3.9 | 3.8 |
| Total | 100 | 100 | 100 |

The average standardised Shannon-Wiener diversity index (J') was highest at Kanyawara (J' = 0.70; 12 months; Potts et al. in press), followed by Sonso (J' = 0.69; 15-months; Newton-Fisher 1999b) and Ngogo (J' = 0.58; 12 months; Potts et al. in press). Using H' data published by Potts (in press) and Newton-Fisher (1999b), matched for calendar months to control for seasonal differences in rainfall, I found that dietary diversity was significantly different between Sonso and Ngogo but not between Sonso and Kanyawara ($N_{Sonso} = N_{Ngogo} = 7$; $t_{1,12} = 4.484$, $p < 0.001$; $N_{Sonso} = N_{Kanyawara} = 12$; $t_{1,22} = 0.385$; $p = 0.704$; independent t-tests).

**Key food species**

At Budongo, four tree species (*Ficus capensis*, *F. mucuso*, *Maesopsis eminii* and *Celtis durandii*) accounted for more than 75% of the time spent eating fruits (equal to 49.4% of the total feeding time). Two more species, *Broussonetia papyrifera* and *C. mildbraedii*, also contributed considerably, albeit mostly due to consumption of their flowers. Adding a seventh species, *Khaya anthotheca*, accounted for over 80% of total feeding time. The top three species, *F. sur*, *B. papyrifera*, and *F. mucuso*, alone accounted for over 50% of feeding time. At Ngogo, the top three species, *F. mucuso*, *Uvariopsis congensis* and *Chrysophyllum albidum* also accounted for over 50% of feeding time. At Kanyawara, the top four species, *F. natalensis*, *F. sansibarica*, *Mimusops bagshawei*, and *Celtis africana*, accounted for over 50% of feeding time. Figs alone accounted for 45.5% of feeding time at Kanyawara, 37.5% at Ngogo, and 36.9% at Sonso (the measure in Kanyawara and Ngogo is based on 100% of the feeding time; the measure at Sonso is based on the time spent on all food species – trees, climber, THV – accounting for a total of 97.7% of feeding time; Table 6.3).

**Non-vegetarian foods**

All three communities have been observed to hunt mammals, including primates (Mitani and Watts 2001; Newton-Fisher et al. 2002; Gilby et al. 2010). Insects are also consumed and sometimes extracted with tools: in particular, a few Ngogo chimpanzees have been observed using twigs to feed on beetles, a behaviour not seen at Kanyawara or Sonso (Sherrow 2005). At Kanyawara and Ngogo, but not at Sonso, chimpanzees use sticks to obtain honey from bee hives (Whiten et al. 1999; Reynolds 2005; Watts 2008; see chapters 4 and 5).

**Other communities within Budongo Forest**

I compared the dietary patterns of two other communities in Budongo Forest (Kaniyo Pabidi and Busingiro). Figs constituted a major component of the diet at both sites although at a lower rate compared to Sonso (Plumptre et al. 1997). Analyses of the field assistants' reports at Kaniyo Pabidi, confirmed the chimpanzees' preference for visiting Ficus trees (28% of visits, N = 337; Table 6.5), particularly *F. mucuso* (N = 180), but also *C. wightii* (N = 117) and *U. congensis* (N = 108), followed by *C. alexandrii* (N = 97) and *C. mildbraedii* (N = 82).

**Table 6.5.** Food preferences in Kaniyo Pabidi extracted from field assistants records with trees represented by dominant genera, expressed as number or percentage of total visits.

| Food | # Visits | % |
|---|---|---|
| *Celtis* | 218 | 18.1 |
| *Cynometra* | 144 | 12.0 |
| *Ficus* | 337 | 28.0 |
| *Chrysophyllum* | 140 | 11.6 |
| *Uvariopsis* | 108 | 8.9 |
| Meat | 33 | 2.7 |
| Insect | 14 | 1.2 |
| Other | 211 | 17.5 |
| Total | 1205 | 100 |

## 4. Discussion

### 4.1. Assessment of the 'local adaptation' hypothesis: Comparison of the Ugandan and Tanzanian chimpanzee communities

Among the Ugandan chimpanzees, the Sonso community has the smallest number of extractive tool-using behaviours of all communities. In particular, stick use is nearly absent, in striking contrast to all other main chimpanzee long-term study sites (Whiten et al. 2001). Although sticks are sometimes manipulated during nest building or play behaviour, they play no role during food acquisition. However, my experimental results also show that the Sonso community is probably not unusual within Budongo forest, since the Busingiro and Kaniyo Pabidi communities do not appear to use sticks either. Although I obtained fewer interactions with the apparatus at these two sites compared to Sonso and Kanyawara, the Kanyawara chimpanzees manufactured sticks from the first day of the experiment (chapters 4 and 5), suggesting that the absence of stick use could be the norm for the estimated 8-10 communities of Budongo Forest. However, some other communities living in fragmented, isolated forests adjacent to Budongo (some 25 km from the main blocks) may use sticks during foraging (Reynolds 2005; Wallis, personal communication; McLennan 2011).

Interestingly, these sites are characterised by poor food availability for chimpanzees, especially if compared to the Sonso area (Reynolds 2005).

More broadly, my analysis shows that Ugandan communities have less extractive tool-using behaviours than other communities of the same subspecies but that they do not differ from them in other tool-using activities. Therefore, they appear as capable of developing tool use as other populations of the same subspecies, but they do not develop them in the same contexts. Second, the Kanyawara and Ngogo communities show different patterns of tool use but they are genetically undistinguishable (Langergraber et al. 2010). Genetics are therefore unlikely to explain these differences, as predicted by the fact that all these communities belong to the *P. t. schweinfurthii* subspecies. The 'local adaptation' scenario altogether is therefore unlikely to explain the tool-using behavioural differences in this case. However, it is also hard to correlate this result with an ecological comparison between all the sites as the Tanzanian sites are all located at the shore of the Tanganyika Lake, offering a very diverse environment encompassing grassland, woodland, and forest (Nishida and Uehara 1981), hardly comparable with the secondary semi-deciduous forests proposed to the three Ugandan communities. Many ecological reasons could therefore account for these differences in food-related tool-using behaviours, as the environments the Ugandan and Tanzanian chimpanzees live in are very different. To investigate the potential role of ecological factors, it is thus necessary to approach the problem at a smaller scale with more comparable sites, such as the secondary forests of Kibale and Budongo in Uganda.

### 4.2. Assessment of the 'ontogenetic flexibility' hypothesis: Comparisons of habitat quality and extractive tool use diversity

My analyses have shown that, despite close proximity and similar histories, the three main study sites at Sonso, Ngogo and Kanyawara are by no means identical in terms of their ecology, no matter how superficially similar they appear at first sight. Although all communities devote large amounts of time to feeding on ripe fruits, most extremely so at Ngogo, followed by Kanyawara and Sonso, there are considerable differences in the availability of fruit trees, even within Kibale Forest. Ngogo has more fruit trees than Kanyawara (Chapman et al. 1997) and, perhaps as a consequence, Kanyawara individuals

rely most extensively on THV (Wrangham et al. 1996; Potts et al. in press). The mesocarp of ripe fruits at Ngogo also contains high concentrations of protein and may in part explain the unusually large group size of the Ngogo community (Mitani and Watts 1999; Hohmann et al. 2010). However, although access to food sources high in protein and carbohydrates is important, diversity may also be a relevant factor (Felton et al. 2009; Raubenheimer et al. 2009), perhaps because it buffers populations against periods of food scarcity. The Sonso chimpanzees have the most diverse food availability and diet of the three communities (Table 6.2), with no record of food scarcity during 15 years of observations (Newton-Fisher 1999b; Reynolds 2005). Individuals devote only 54.5 to 70.0% of their feeding time to ripe fruits (Tweheyo et al. 2004), but consume nearly twice as many items compared to both Kibale communities. The diet at Sonso also contains a high proportion of a non-native species, *B. papyrifera*, from which all parts are being eaten because they are free of tannins and thus offer readily-digestible sugars (Reynolds et al. 1998). Comparing Shannon-Wiener indices suggests that Kanyawara and Sonso chimpanzees have a similar dietary diversity, but my analysis shows that the two diets differ in quality. At Kanyawara, the diversity is largely due to THV, while at Sonso, it is due to leaves and flowers (Reynolds 2005). Kanyawara chimpanzees thus appear to have the least favourable environment and need to complement their diet with THV on a monthly basis (Wrangham et al. 1996). In comparison, Ngogo chimpanzees have a richer habitat with a large number of fruit trees, which account for more than 80% of their feeding time. Although a rich diet, this extreme reliance on fruits may expose chimpanzees to periods of fruit shortage if the pattern of fruiting does not guarantee that at any time of the year, some fruits will be available (although the high density of fruit trees in this area could in theory prevent that). Finally, Sonso chimpanzees, while eating fewer fruits, have a very broad diet, which includes many different species and types of foods such as flowers, leaves and seeds, which could protect them from food shortages.

Could these ecological differences be related to observed differences in tool use? At the scale of Uganda, the Sonso, Kanyawara and Ngogo communities all live in comparable secondary forests, and given their close genetics, the observed variation in extractive behaviours could depend on smaller variations between environments, which influence especially the general diversity and quality found in chimpanzee diet. The relationship between tool use and ecology has already been suggested in other study sites. In Bossou, notably, it has been suggested that nut-cracking was necessary to cope with low food availability periods (Yamakoshi 1998, 2001). An interesting parallel can also be drawn with Sumatran

orangutans. In Ketambe, orangutans consume strangler figs as part of their diet. Although these fruits are considered fallback food in comparison to other fruits, they are present throughout the year, assuring the Ketambe orangutans a constant supply (Morrogh-Bernard et al. 2009). Similarly to the Sonso community, this community has been found to have a very small tool catalogue in comparison with other orangutan communities (van Schaik 2009). However, the results I found appear to be in conflict with the predictions of the 'ontogenetic flexibility' hypothesis. Under this hypothesis, the ecology plays a major role in the shaping of behaviours in chimpanzees and assumes that the conditions faced by an individual will trigger the development of certain behaviours in response to this environment. However, the Kanyawara community, which appears to live in a less favourable environment (as they need to complement their diet with THV), does not have as many food-related tool-using behaviours as the Ngogo community that lives in the environment with the best food quality. Therefore, the current ecological conditions appear to be poor predictors of which feeding-related tool-using behaviours are found in the study communities. More likely, my data support the general hypothesis that ape communities with a broad choice of feeding possibilities will need to rely less on extractive techniques compared to communities that face periods of food shortage. As a consequence, the former may have less food related tool-using behaviours than the latter. In particular, communities such as the Sonso community, which consumes several different qualitatively rich plant items such as flowers or seeds, may always find an easily accessible food within reach, reducing drastically their need to keep in their behavioural repertoire cognitively complex behaviours such as food-extractive tool-using behaviours.

### 4.3. The 'cultural diversity' hypothesis: Innovation and loss of behavioural traditions in relation to forests' evolutionary history

In the following section, I review the evolutionary history of Kibale and Budongo forests in relation to the evolution of their chimpanzee communities in an attempt to explain their differences in tool use. The subspecies *P. t. schweinfurthii* has low genetic diversity (Goldberg 1996; Goldberg and Ruvolo 1997b), suggesting that genetic differences are unlikely to explain the observed behavioural differences. The absence of stick use in some Budongo communities is even less likely to have a genetic explanation given that other

communities less than 30 km away appear to use sticks during food acquisition (McLennan 2011). However, what cannot be ruled out is that ecological fluctuations in the recent past may have been responsible for the current distribution of stick use as well as behavioural differences more generally. Many chimpanzee communities in Uganda and elsewhere in Africa use sticks as tools (Whiten et al. 2001). The behaviour appears to develop easily under laboratory conditions (Tennie et al. 2009) but, for unknown reasons, probably not so easily under natural conditions (see chapter 5). Given these last results, the most parsimonious interpretation is that stick use was not invented in many independent occasions in the Ugandan populations but was probably present in the East African population ancestral to the current communities of Kibale and Budongo Forest, which probably had a tool catalogue as developed as the Tanzanian populations. During the last Ice Age, the chimpanzee population was indeed coping with a harsher environment in which food was potentially more difficult to access, and this may have favoured various behavioural innovations. During the subsequent warmer periods of reforestation, the Budongo area gradually became a *Cynometra*-dominant forest (Howard 1991; Plumptre 1996), whose seeds are a major food source for chimpanzees (Reynolds et al. 1998). This tree species, along with a number of others, is absent at Kibale. Therefore, one scenario is that the original colonisers of Budongo Forest were able to expand and diversify their diet, and tool-based food acquisition probably became less important throughout Budongo Forest to the point of being lost (see Wrangham 2006 for a similar point regarding nut-smashing). On the contrary, the lower item diversity (in Ngogo) or lower food quality (in Kanyawara) of the diet in Kibale may have prevented this extinction, although other behaviours such as termite fishing may have disappeared at Kanyawara because of the absence of the preyed species (Whiten et al. 2001).

It is difficult to speculate on the exact timing of the loss of stick-use throughout Budongo Forest. On the one hand, climatic changes led to more favourable habitats for chimpanzees throughout Africa. More recent anthropogenic changes in Budongo, particularly through logging, resulted in considerable expansion of secondary forest growth, including fig species, which are excellent primate foods (Plumptre 1996). At Sonso, another by-product of logging was the introduction of *B. papyrifera*, which has become a highly preferred food tree because of its easily-digestible parts (Reynolds et al. 1998). Busingiro was also logged, suggesting that the food availability was similarly broad and favourable for chimpanzees (Plumptre et al. 1997). However, Kaniyo Pabidi, the third site within Budongo Forest where stick use is allegedly absent, was never logged, and consequently has lower forest diversity than Sonso

and Busingiro. Interestingly, the forest fragments around Budongo, such as Kasokwa or Bulindi, have a much less diverse flora than the main forest blocks and its chimpanzee communities appear to use sticks during foraging (Reynolds 2005; McLennan 2011). Chimpanzees in these areas may have either never lost or re-invented the behaviour, although the second hypothesis is less likely given chimpanzees' apparent limitations in developing stick use (chapter 5). Based on these findings, the loss of stick use may be a more ancient event, perhaps dating back to the initial colonisation period of the forest.

In conclusion, my analysis of the different hypotheses shows that the cultural diversity scenario is the most plausible one. However, the forests' histories and the patterns of tool-using practices suggest that ecology plays a role in the emergence and disappearance of cultural differences, but not in their maintenance within a group. The study presented in this chapter shows that the ecological influence on the development of tool-using behaviours is not simple to analyse and, thus, that we should remain cautious in assuming that different ecological conditions may be responsible for the development of different tool-using behaviours at each new generation. Adopting such as stance appears to conflict with the data I presented in this chapter: while there are notable ecological differences between sites currently, they appear unconnected to the observed variation found in tool-using behaviours. In other words, treating ecology as a factor that triggers at each generation the development of a certain pattern of behaviours appears erroneous. On the contrary, the data I presented in this chapter support an evolutionary model that links the evolution of tool-using behaviours to the evolution of environmental conditions on a longer scale basis and supports the view of ecology as a selective force acting on behaviours.

# Chapter seven: General discussion

"The passing of every old man or woman means the passing of some tradition, some knowledge of sacred rites possessed by no other... The information that is to be gathered for the benefit of future generations... must be collected at once or the opportunity will be lost for all time"

Edward Sheriff Curtis (1907)

"Par ma foi ! il y a plus de quarante ans que je dis de la prose sans que j'en susse rien, et je vous suis le plus obligé du monde de m'avoir appris cela."

*Le Bourgeois-Gentilhomme, Acte II, scène 4,* Molière (1670)

[ "By my faith! For more than forty years I have been speaking prose without knowing anything about it, and I am much obliged to you for having taught me that." The Gutenberg Project, translation by Philip Dwight Jones]

Parts of this chapter are in preparation for submission in the following review paper:

**Gruber, T.** & Zuberbühler, K. The Jourdain hypothesis: Chimpanzees have culture, but they don't know that they do. *In prep.*

and submitted as the following research paper:

**Gruber, T.,** Krupenye, C., Byrne, M.-R., Mackworth-Young, C. McGrew, W.C., Reynolds, V. & Zuberbühler, K. The influence of ecology on chimpanzee cultural behaviour: A case study of five Ugandan chimpanzee communities. *Submitted*.

## Summary

In this final chapter, I summarise the findings of my work and relate them to the problems I have presented in the general introduction. Firstly, I discuss how the methods I have used can bring meaningful answers to the debates currently taking place in cultural primatology. In particular, my field experiments have contributed to assess experimentally the exclusion method directly in the field. To do so, I have tested if chimpanzees of different communities, which resemble each other sufficiently in terms of genetics and the environment they live in still differ in their tool-using behaviours. My results have shown that community-specific behavioural differences can be found even if the other main variables are kept constant, suggesting a role for culture. Based on these results, I address the point of whether animal cultures can be studied by estimating the contribution of genetic, ecological, and social factors to observed behavioural differences between groups. Rather than attempting to single out one origin for the behavioural variation, I present a model where each factor is involved in the development of tool-using behaviours and cultural differences.

However, I show that such a model will not solve the cultural debate, as most human researchers will not accept a behavioural definition of culture as used by animal researchers. Thus, I propose to adopt a more cognitive approach to the study of animal cultures, and directly assess if animal cultures can be considered as conglomerates of ideas rather than behaviours as in humans. My results indeed suggest that chimpanzees are not only 'cultural animals', but that they also have a 'cultural mind', which influences how they perceive and deal with their environment. Such a framework of ideas makes it possible to solve some of the controversies of the cultural debate, notably the asocial/social learning opposition, and to integrate this debate in a general reflection on the evolution of intelligence.

More generally, adopting a cognitive stance may allow researchers to pinpoint more clearly the differences between animal and human cultures. Finally, I present the limitations of my work, how they could be addressed, and what future studies should be conducted within the cognitive framework I propose, towards the more general objective of understanding what makes human culture uniquely different from chimpanzee culture.

## Objectives and general findings

Considering the fact that chimpanzees are widely seen as the most complex tool-users within the animal kingdom (Beck 1980; Shumaker et al. 2011), it is puzzling to observe that the Sonso chimpanzees are very limited in their tool-using abilities (Reynolds 2005). More generally, Ugandan chimpanzee populations appear to be limited in their tool use repertoire when compared to other populations (McGrew 2010), a finding that could result from genetic or environmental differences or both. This simple fact is at the core of this thesis and in this chapter, I engage with the current cultural debate by investigating the factors that influence the development of behaviours in animals. Genetics, environment and culture, defined as any transfer of information through socially-aided means, are all presumed to influence behaviours, and in this thesis, I sought to study the impact of each of these factors.

Firstly, I studied how genetics played in the development of tool use by observing wild-born captive bonobos in a sanctuary in Africa (chapter 3). The bonobo, although closely related to the chimpanzee, has long been described as a poor tool-user, a characteristic that has been thought to be the major difference between the two sister species (McGrew 1998). However, I was able to show that their tool-using abilities did not differ from that of captive chimpanzees and that bonobos, as much as chimpanzees, could develop tool use if the right conditions were present. Considering the numerous reports on chimpanzees' abilities to use tools, this chapter suggests that the general genetic predispositions required for understanding tool use is already present in the common ancestor between bonobos and chimpanzees. If this is correct, then it is unlikely that the inability of the Sonso chimpanzees to use tools has genetic reasons.

In the case of wild bonobos and Ugandan chimpanzees, while genetics are unlikely to explain their apparent limitations in tool use, their environment is a likely cause. By closely comparing ecological data and tool use behaviours, I showed in chapter 6 that ecological explanations on their own were unlikely to be sufficient to account for chimpanzees' tool use limitations. Although I found, as expected, a number of ecological differences between sites, they were not correlated with the current observed differences in tool use. In order to explain my results, and more generally, to attempt to understand the role of ecology in the cultural phenomenon, I have developed in this chapter the idea that ecology may influence the development of tool-using behaviours differently than through individual plasticity. As such,

ecology appears to influence cultural behaviours, not by triggering the development of these behaviours in each individual independently, as predicted by the 'ontogenetic flexibility' hypothesis, but rather by having a more 'temporal' effect: the conditions that a certain community are facing will trigger the appearance, maintenance and disappearance of the behaviours depending on if these behaviours are needed to survive in their environment. However, the transmission of these behaviours within a community may only owe to social learning processes, making them cultural *in fine*.

Finally, it remained to be seen if culture could cause differences in tool-using behaviours between groups. The widely used 'exclusion method' is based on the idea that cultural variants can be isolated by determining behaviours for which group-specific variation is unlikely to be the result of genetic or ecological influences (Whiten et al. 1999). The method has remained controversial, however, largely because it provides no direct evidence for the presence of key components of most definitions of culture, i.e. social learning and traditions, other than by parsimony (Laland and Janik 2006). Observing that in humans, cultures drive their practitioners to adopt particular behaviours or attitudes to solve particular tasks, I predicted that if tool use differences in chimpanzees were caused by differences in culture (i.e., cultural knowledge), then individuals of different communities with different knowledge should react differently to an identical tool use task. To address this, I took advantage of the limited tool repertoire of the Sonso community. I assumed that these chimpanzees, who have never been observed using sticks during food acquisition over the last twenty years, would use a different method to extract inaccessible honey compared to groups that use sticks habitually. Specifically, the Kanyawara community, also situated in Uganda, possesses the presumed cultural variant 'fluid-dip' according to Whiten et al. (1999), predicting that individuals of this community would rely on this knowledge to solve the task. On the contrary, if chimpanzees were not influenced by their cultural knowledge but only driven by the affordances of their environment, then all subjects, regardless of their community membership, would react in similar ways to the task if it was being kept constant.

In chapters 4 and 5, I have shown a strong community-specific segregation in tool use in individuals who were free to select the solution they wanted to access the honey. This finding was the same even when a suitable tool was provided. Both experiments thus showed that chimpanzees were relying on their knowledge when dealing with constraints imposed by their environment. Additionally, the community-specific segregation in behaviour showed that this knowledge could be defined as cultural. Chapter 5, finally, showed that chimpanzees

could be constrained by such cultural knowledge in that they could not overcome their preferences or lack of interest for some particular parts of their environment to discover and experiment with new solutions. Taken together, these results suggest, firstly, that geographical differences in tool use reflect geographical differences in knowledge, which is in turn largely acquired through social learning, making these differences cultural. Secondly, these studies show that chimpanzee 'conservatism' can be extreme, even when the relevant skill is absent. In other words, chimpanzees' previous knowledge appears to constrain and prevent them from learning novel techniques. As such, a social influence may be the only way to highlight the salience of some parts of chimpanzees' environment.

In the following sections, my goal is to develop a model of how different factors can influence the development of flexible behaviours. The core feature of this model is to go beyond the documented behavioural level and to include a cognitive dimension, in order to encompass more fully the phenomena at issue.

## A. Animal behavioural variation: A conglomerate of influences

### 1. Evaluation of the exclusion method

#### Addressing the critics

In chapter 1, I showed that the exclusion method, often used as a means to show culture in wild populations (Whiten et al. 1999; Rendell and Whitehead 2001; van Schaik et al. 2003), suffers from a number of flaws, as outlined by Laland and Janik (2006, 2007). A key point is that genetic and environmental influences cannot be considered as independent as they interact with each other. The concept of 'exclusion', however, presupposes that different factors can be analysed and discarded on their own if they are thought to impact on two populations in similar ways. The same authors also question the "seriousness" (Laland and Janik 2006, p. 545) with which alternative genetic and ecological hypotheses are usually tested in studies aimed to explain group-specific variations of behaviour. This point enjoys some thrust by the fact that one third of the observed behavioural variants in chimpanzees are

only found in one subspecies (*P. t. verus*), which is significantly different from the other subspecies at the genetic level (Morin et al. 1994; Gagneux et al. 1999). This is a relevant finding because a recent study has shown a correlation between cultural and genetic variation in chimpanzees (Langergraber et al. 2010).

A similar point has been made regarding the ecological differences (Galef 2009). It is true that researchers will never be able to discover all of the differences between two or more environments. However, a careful comparative analysis of the most relevant differences and the quantification of the variation of certain tool behaviours, such has been done with nut-cracking or ant-fishing in chimpanzees (McGrew et al. 1997; Möbius et al. 2008; Schöning et al. 2008), should be able to isolate the key ecological influences. It is indeed as meaningless to consider that no ecological difference has an impact on tool-using behaviours as to think that any single difference, even unrelated to the context considered, would have an effect on the presence of a behaviour (for instance, the presence of say, a certain type of shrub, on the development of nut-cracking in wild populations of chimpanzees). As such, if genetic and environmental influences can be controlled for between some populations, then a potential impact of the cultural effect can be evaluated. Observational data, however, may not be strong enough to support such a statement.

**Field experiments and statistics as a solution to assess the cultural nature of behaviours**

Field experiments, in contrast to observational data, allow some control over environmental influences and the subjects that are being tested. While genetic differences can play a possible role in the behavioural variation observed between communities that are separated by thousands of kilometres and that have been isolated from each other for hundreds of thousands of years, they are less important when trying to explain differences between communities of the same subspecies. Genetics are even less relevant when the communities are separated from each other by a few hundred kilometres and share most of their evolutionary history. Implementing ‘outdoor laboratories’ such as pioneered by Matsuzawa (1994) at two different sites allows researchers to control for the ecological affordances of the study site at the time of the experiment. If the experiment consists of a novel stimulus or apparatus unfamiliar to the individuals, then the affordances will be the same for all individuals, even if they belong to different communities. In summary, although the influence

of genetics and ecology can never be completely ruled out or discarded, they can be controlled for to a large degree by implementing suitable experimental methods.

Field experiments have been used to study social learning in a number of animals but never in chimpanzees, most likely because of practical difficulties (Reader and Biro 2010). If a behaviour is experimentally introduced, its spread throughout the community can be subsequently followed in a more controlled way than with natural observations. This is because innovations in the wild are rare and most of the time it is impossible to determine if the newly observed behaviour has simply been overlooked by the researcher beforehand (Reader and Laland 2003), a problem that is absent with an artificially introduced behaviour.

Despite the previously mentioned problems of natural observations to support claims of culture, they are crucial when selecting the experimental task. Tool-using activities are often amongst the last activities observed by researchers as they require high degrees of habituation in wild populations (e.g. Boesch and Boesch-Achermann 2000). Long-term observational data are thus important to ensure that presumed cultural differences are not the result of differences in observational efforts. The selection of 'fluid-dip' as the key behaviour to test between the Sonso and Kanyawara groups was based on the surprising observation that no chimpanzee at Sonso had been observed using sticks during food acquisition over twenty years of observations. Additionally, the field experiment must be designed to allow for a realistic implementation in a wild setting (Zuberbühler and Wittig 2011). In this respect, if any of the Sonso individuals had developed stick use during the later part of the experiments (chapter 5), this would have probably qualified as an innovation, given the surprising reluctance of wild chimpanzees to experiment with novel behaviours. Hence, field experiments of the kind described in chapters 4 and 5 can also have a secondary benefit: they allow researchers to confirm that a key behaviour is truly absent in the group's repertoire, if this has already been suggested by observational data.

However, even if no novel behaviour develops, the cultural effect can still be inferred from the distribution of behaviours between communities, based on the assumption that social learning will result in a higher homogeneity of behaviours within rather than between communities (Kendal et al. 2009; Laland et al. 2009). The results I obtained both in chapter 4 (hole affordances) and chapter 5 (tool affordances) showed an absolute segregation of behaviours between the two communities, supporting strongly a cultural influence. Such results could not have been obtained if individuals had developed their solution on an ad-hoc

basis, while encountering the task, assuming that each solution had an equal likelihood to be developed (see chapter 5). However, it could still be claimed that each individual independently developed the solution prior to the experiment, and simply applied this knowledge to the task when encountering it. This criticism can be addressed by designing a task that is sufficiently new to the subjects that they cannot transfer their behaviour across conditions (Call and Tennie 2009; Tennie et al. 2009).

Field experiments can be used to study each of the factors influencing the development of behaviours, by controlling the others and only allowing one variable to vary. However, this reasoning still occurs in a framework where the three influences are being separated. In the following sections, I present a view in which genetics and ecological influences are considered in a manner that would not conflict with the potential cultural influence altogether.

## 2. Genetically programmed to be flexible

### Big brains are useful for tool use

Animals differ in their relative brain sizes (Harvey and Krebs 1990). In recent years, a number of models have emerged to explain why a number of species have bigger brains than others (Isler and van Schaik 2009; Sol 2009). For instance, the cognitive buffer hypothesis states that organisms evolved big brains to cope with environmental unpredictability, a bigger brain allowing them to cope better with the fluctuations of their environment (Sol 2009). Other models, such as the expensive brain hypothesis (Isler and van Schaik 2009) or the maternal energy hypothesis (Barrickman et al. 2008) put the emphasis on development: species with big brains either had to relocate energy from other organs (for instance the pectoral muscle in birds, Isler and van Schaik 2006) or access new sources of energy. The study of maternal impact on pre- and post-natal brain development has also shown a positive correlation between brain development and the length of gestation and lactation respectively (Barton and Capellini 2011). Although this last study did not support the cognitive buffer hypothesis (see also van Woerden et al. 2010), its authors emphasise that the different theories are not mutually exclusive. More generally, studies show a positive correlation between brain size and life span for which the causal direction is hard to predict (Gonzalez-

Lagos et al. 2010). An interesting by-product of the extended life span typically associated with having a big brain, is that this also leads to longer maternal investment, delayed reproduction, and longer contact with offspring (Covas and Griesser 2007). As a consequence, offspring are exposed longer to parental behaviours. This highlights another intrinsic link between social learning, large relative brain size and enhanced cognitive abilities (Deaner et al. 2007). Hominoids are characterised by their unusually large relative brain size in comparison with other primates, suggesting that this feature has enhanced their abilities for tool-using behaviours.

Brain size is positively correlated with the number of cognitive abilities in various groups of animals (Lefebvre et al. 2004) but there is still a debate about whether specific brain structures are responsible for these extended abilities. While Reader and Laland (2002), in primates, and Lefebvre and colleagues (2002) in birds, found that cognitive abilities correlated with the size of certain parts of the brain (i.e., neocortex and striatum in primates and the equivalent neostriatum structure in birds), Deaner and colleagues (2007) showed that total brain size predicted general cognitive abilities as much as neocortex ratio in primates and argued that could be the result of the functional integration of different parts of the brain.

In primates, larger brains are correlated with a higher innovation rate, more tool use, enhanced individual learning and more frequent social learning (Reader and Laland 2002). Interestingly, within the primate order, tool use has a non-random distribution, notably regarding food-related tool-using behaviours (van Schaik et al. 1999). Using objects as projectiles is fairly common, but using them as tools to access food is only observed in a few genera. Moreover, most records of monkey tool use behaviour are anecdotal and generally rare, apart from some subspecies of macaque and capuchin monkeys (van Schaik et al. 1999; see chapter 1). Although a number of monkey species can be taught to use tools in captivity, only capuchins, orangutans and chimpanzees have been observed to spontaneously use feeding tools on a regular basis in the wild. Incidentally, these species have some of the biggest encephalisation ratios of all primates (Aiello and Dean 1990).

**Tool use is flexible in apes**

Compared to monkeys, tool use in chimpanzees and orangutans is much more diverse and observed in a multitude of contexts. Some tool-using behaviours occur in social contexts,

such as the leaf-enhanced kiss-squeak in orangutans or leaf-stripping in chimpanzees. In both cases, the physical properties of the tool are used to enhance the conspicuousness of the signal. Secondly, the domains in which this flexibility is expressed can differ between communities of the same subspecies (chapter 6). Ugandan chimpanzees have as many tool-using behaviours in non-feeding contexts as Tanzanian chimpanzees, suggesting that the difference observed in their feeding tool-using techniques does not result from different abilities to develop tool use but may be a reflection of their needs and responses to their respective environments. As all these populations are descendants of the same small population that occupied the Great Rift region during the last Ice Age, the Ugandan communities may have lost some of their behavioural techniques, whilst their general genetic abilities to develop tool use are likely to have remained intact (see chapter 6).

Similarly, bonobo tool-using abilities appear ancient and their limited tool use in the wild cannot be accounted for by genetic constraints. Although a number of studies have documented the tool-using abilities of bonobos (Jordan 1982; Toth et al. 1993; Ingmanson 1996; Gold 2002), chimpanzees have long been considered the prime ape tool users, and, in particular, the best models to study the origins of human culture. The difference may result notably from the limited number of studies involving bonobos (Hare 2009). In chapter 3, I have shown that bonobos are equivalent tool-users to chimpanzees in most contexts and that bonobo tool use has the same sex bias as in chimpanzees (McGrew 1979). As no sexual bias has been described for orangutans (van Schaik et al. 2009b) and since the data for gorillas are too limited, it is hard to speculate about the time when this bias appeared. In any case, results presented in chapter 3 indicate that bonobos possess the genetic predispositions to develop tool use, and that they can be as flexible as chimpanzees. As argued above, the selection of these abilities probably happened before the split between chimpanzees and bonobos, but may even date to more ancient primate lineages.

## 3. Ecology as a selective force on cultural behaviours

### Current views on the ecological influence on the development of tool use

The role of the environment lies very much at the heart of current discussion on animal culture, as outlined earlier (Galef 2009; Tomasello 2009; Whiten 2009). Proponents of a

strong role for ecology in the formation of behavioural differences usually include an ontogenetic dimension, which considers the particular ecological settings of a site as an active generator of behaviour. The basic claim is that encountering a particular setting, such as 'broken nuts, rocks and anvil in the same place', will be enough to trigger the development of behavioural differences, such as nut-cracking behaviour in chimpanzees (Tennie et al. 2009, see chapter 5). On the contrary, in sites where the key components are absent (e.g., nuts), the behaviour will simply not develop. Therefore, in this view, ecology is an active factor that will directly influence the development of certain tool-using behaviours in each individual at each new generation.

The results I presented in chapters 4 and 5 show that this view may be inaccurate. Firstly, this hypothesis takes as a premise that all chimpanzees from any community will react the same to their environment, as far as the affordances of the environment are the same. However, this is not the case, as illustrated by the Sonso/Kanyawara comparison, with the introduction of a novel apparatus. Thus, current settings of the environment are unlikely to trigger individuals to use particular behaviours over others. Regarding how ecology shaped the knowledge with which each individual approached the task, all individuals who engaged with the task appeared to know about honey already, so they most likely had already faced it in their natural environment. Given that the same genera of bees are found in the two forests, the subjects should have faced the same relevant ecological conditions to develop tool use, but they still varied in their response to the task, suggesting that ecology is not enough to explain this variation. However, again, this view presupposes that ecology would be directly responsible for the development of a behaviour in each individual. Rather, in the following section, I favour the view that there is an indirect influence of ecology on behaviours.

**A not-so-novel view of the dynamic role of ecology in the development of tool use**

The data that I presented in chapter 6 show that current ecological settings are poor predictors of tool-using behaviours in chimpanzees. Hence, even though the Ngogo diet appears to be highest in quality, the chimpanzees of this community have the largest number of food-related tool-using behaviours among the three studied communities. Additionally, in chapter 5, I have shown that wild chimpanzees do not develop new behaviours easily. Taking an evolutionary point of view, the history of Ugandan forests allows me to sketch a scenario that accounts for these two results. Tool use in chimpanzees most likely did not emerge

easily in different areas, especially when they are so closely related, as in the case of the different communities that occupy Western Uganda. Rather, the original chimpanzee population likely experienced a harsh environment and did not stay in forest refugia (Goldberg 1996; Goldberg and Ruvolo 1997a, b). These conditions probably fostered the development of innovations in food-extractive behaviours. Although the scenario I present here is speculative, the data suggest that the original chimpanzee population may have had stick use in their tool repertoire, as it is being found in almost all studied Eastern chimpanzee communities, apart from Budongo. The other possible scenario is that each of these communities developed the behaviour individually, due to individual innovation. However, this scenario is at odds with the difficulty that chimpanzees face in understanding the functional properties of sticks in the absence of social models, as illustrated in Chapters 4 and 5. Therefore, the cultural scenario seems more parsimonious. Of course, it is not possible to reconstruct events that have happened 8,000 years ago (e.g., stick use may have disappeared and reappeared several times in the different communities). The main goal of chapter 6 is to illustrate how ecology can play a role in the generation of cultural variants, which are then maintained by transmission through social learning processes.

Investigating the relationship between ecology and tool use is only taking a particular case of investigating the relationship between ecology and behaviour in general. Darwin's theory of natural selection (Darwin 1859/1993) consists of studying how particular behaviours are selected at a certain point because they are adaptive to cope with the environment that the organism displaying them faces. Therefore, the view I adopt here to explain the influence of ecology on the development of tool use is one of a selective force that will select any behaviour that reveals itself more adaptive than other behaviours. When environmental settings change, the pressure on the maintenance of the different behaviours also changes, which may result in the disappearance of behaviours. Adopting this view allows one to put the emphasis on the dynamic characteristic of this phenomenon: food-related cultural behaviours appear and disappear in conjunction with ecological variations. This approach also limits the extent to which ecology as an active shaper of behaviour should be relied on when accounting for cultural differences. While it has been argued that the ecology can trigger the development of specific behaviours in each individuals at each generation (Tomasello 2009), ecology seen as a selective force does not require this demanding condition, and therefore appears altogether less cognitively demanding.

## 4. Conclusion: Adaptiveness and limitations of the 'three-influence' model to the problem of culture

The empirical results I have presented in this thesis are hard to analyse if the focus is put on trying to attribute some of the variation to a particular factor. For instance, it is unlikely that the behavioural differences between the chimpanzees at Kanyawara and Ngogo, which are genetically undistinguishable (Langergraber et al. 2010), have a genetic origin. Thus, these differences must be explained in non-genetic terms. Although in close proximity, the two sites are very different in their ecology and dietary diversity (Potts et al. in press). Similarly the differences in food-related tool-using behaviours between the three Ugandan communities hardly correlate with their current environment. Attempting to elucidate the influence of ecology and culture as two competing factors on tool use diversity thus is unproductive. Rather, here, I favour a model where genetic, ecological and social factors all influence the development of tool use.

In terms of genetics, primates have very advanced manipulative skills and chimpanzees are generally motivated to interact with their physical environment. Whether some of these skills are adaptations that have been selected in response to climate-induced habitat fluctuations is a hypothesis that will require further investigation. Another characteristic useful in tool use is the ability to learn socially from each other (Whiten et al. 2009). Again, it is hard to decide whether natural selection has directly favoured this cognitive ability, or whether it is a mere by-product of other biological changes. Yet, social learning appears adaptive in a range of animals (Laland 2001). Secondly, it is likely that during the most recent reforestation period, ecological pressures decreased for chimpanzees, although not all areas may have been affected equally. The chimpanzees who colonised the area that would become Budongo Forest during reforestation probably accessed a high quality environment, which, in the recent past, became even richer due to secondary forestation following the selective logging activities within parts of Budongo Forest. Based on my empirical results and review in chapter 6, my general hypothesis is that the resulting increase in dietary diversity led to a loss of cultural diversity in the Budongo chimpanzees, which included the loss of stick use. Whether the proposed scenario can explain the behavioural differences in other chimpanzee or ape communities remains to be tested. It is unlikely that a general comparison at the species level can be conducted, as the environments in which the animals are found differ too

much. However, at the local level, it may be possible to assess the impact of ecology on tool-using behaviours for each particular ecological situation. For instance, a similar scenario may have happened with the bonobo populations: their geographic isolation in a rich environment (Badrian and Malenky 1984) may have prevented them from developing food-extracting tool-using behaviours, a hypothesis that remains to be tested.

Finally, socio-cognitive factors are likely to have reinforced and maintained this effect throughout the entire forest. If youngsters no longer witness their mothers' handling of sticks, they are less likely to develop an interest in sticks which will therefore prevent them from learning to use sticks as tools. In chapter 5, I have shown how Sonso chimpanzees appear to regard sticks as irrelevant pieces of vegetation, not as items with a functional importance. In sum, the loss of stick use may have initially been caused by ecological factors while the sustained absence and complete disappearance throughout Budongo is probably best explained by social learning and cognitive factors, which prevent wild chimpanzees from performing certain behaviours (Wrangham 2006). This hypothesis is supported by the fact that Budongo chimpanzees raised in a sanctuary from an early age, readily learn tool use from their keepers (Marshall-Pescini and Whiten 2008).

In conclusion, genetics, ecology and social cognition may all contribute in different ways to the observed behavioural differences in wild groups. Genetic factors appear to explain a species' main propensity to manipulate objects, discover their value as tools and learn new behaviours socially from each other. Genetics would thus intervene in the global capability of a species to develop novel behaviours. Ecology acts as a selective pressure on behaviours. Certain adaptive behaviours, such as food-extractive tool use behaviours, will be selected for in harsher environmental conditions. However, they can potentially disappear if these conditions change and favour easily accessible foods over hard-to-process ones. Therefore, ecology plays a constant role in the maintenance of behaviours, in that any environmental change can make a trait more advantageous (for instance, during a period of food shortage) or on the contrary, unnecessary. However, the maintenance of the behaviour at the community level is most likely done through social learning processes. The Budongo chimpanzees show by their surprising refusal to develop stick behaviour in an experimental setting that it seems to be hard for a chimpanzee, even if given the 'right' ecological conditions, to develop stick use on its own. Considering that this behaviour is seemingly simple even from a chimpanzee perspective (it does not include several steps such as nut-cracking for instance), it is even less likely that complex behaviours can be learnt individually by chimpanzees without witnessing

a model. Thus, socio-cultural skills may be necessary to maintain a behaviour within a repertoire. Although some 'genius' individuals may be needed to develop new behaviours, these new traits can only become adaptive for populations if they can be transmitted, and primate social skills and abilities to learn from each others are most likely the only way to do so. In summary, genetic and ecological influences are necessary for the emergence of cultural behaviours, which are being transmitted by individuals thanks to their social predispositions.

## 5. Transition: A behaviour-based model will not end the debate on animal culture

Over the last twenty years, the question of animal culture has fostered much debate, particularly under the influence of Galef (e.g. Galef 1992) and Tomasello (e.g. Tomasello 1990), which some have referred to as a "war" (McGrew 2003). After two decades of debates, the situation tends now towards more agreements, to the extent that some commentators see something of a peace coming (Sterelny 2009). However, my analysis of the different positions has shown that the situation is more of a ceasefire than a real peace: the two parties appear to have come to a point where there is not much more that can be done to find out how much human-like animal cultures are. It is likely that, with the multiplicity of long-term field sites and of resulting observations, reports of novel behaviours will emerge and researchers will be able to follow their dissemination throughout the community (Nishida et al. 2009), documenting the role of social influences in the transmission process. Similarly, successful field experiments will probably help in seeding new behaviours in wild chimpanzee communities and will help to confirm the existence of the social influence in the establishment of these behaviours as well. However, although necessary and long awaited, these results will not end the debate on animal cultures, as long as they are only considered as conglomerates of behaviours. Although we may reach a point where the weight of each influence can be measured and determine which behaviours depend in part on social learning, making them cultural by the definition adopted by most animal researchers (Fragaszy and Perry 2003a), these results will not bring any answer to the fundamental question of knowing if animals 'feel' cultural as much as humans do (in the sense that they would attach a meaning to their practices, and be willing to fight for them as markers of their membership of a social group). In the first place, a definition based on behaviours does not allow us to ask such questions, as behaviours are only described at the superficial level. In

other words, it is impossible to ask if chimpanzees have a 'cultural mind'. In the next part, I introduce a shift of paradigm and ask if rather than analysing animal cultures as conglomerates of behaviours, researchers should not analyse them as conglomerates of ideas, which will trigger a whole range of new study questions.

## B. A cognitive approach to the study of culture

### 1. A world of ideas acquired socially

#### A shift of paradigm: Replacing patterns of behaviours with patterns of ideas

The difference in approaches to culture between social anthropologists and animal researchers has led to the idea that cultures in animals and humans are different in kind (Galef 2009; Hill 2009; Tomasello 2009). Primatologists and most animal researchers use a definition of culture that is based on a conglomerate of behaviours that qualify as traditions. For example, a widely accepted definition proposed by Fragaszy and Perry (2003a, p. xiii) is that a tradition is "a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning". On the other hand, anthropologists rely on a definition of culture as a conglomerate of ideas such as "a historically derived set of shared ideas, values, norms, and beliefs that underlie behavior" (Hill 2009, p. 279). This divergence in emphasis may explain the lack of interest of social anthropologists for the study of animal cultures (Perry 2009). However, this distinction comes only from a difference in methodology, as most data on wild animals are observational and often not strong enough to enable a deeper analysis, including questions about underlying cognitive processes. However, recent field experiments, including the ones I have presented in chapters 4 and 5, provide more controlled data, which allow researchers to address questions at the cognitive level (Biro et al. 2003; Reader and Biro 2010). I will use the term 'idea' in the sense of 'mental representation' understood as the "stored form derived from experience which is used to generate action" (Bryson 2009). For instance, the idea of 'stick use' is a representation that contains the object stick and its functional property as a tool for specific actions.

As already highlighted in the previous empirical chapters, my experiments support the idea of an important cognitive dimension in chimpanzee cultures. First, chapter 4 showed that chimpanzees react to new tasks in their environment by using previously stored knowledge, in ways that suggest it to be cultural. In chapter 5, I showed that exposing the Sonso chimpanzees to stick usage, even when most of them had not succeeded in gathering honey as they did not find a tool solution of their own, did not foster the development of this behaviour. Rather than assuming that chimpanzees were cognitively limited, which was not supported by work conducted in captivity, I proposed the hypothesis that chimpanzees were cognitively channelled during their ontogenetic development and that sticks had become irrelevant parts of their environment. This cognitive channelling appears also to be cultural, as all individuals of a given community reacted to the same part of the tool I proposed, while ignoring the other parts. In this respect, what I found comes close to the notion of a cultural override that was introduced for humans (Haun et al. 2006b). According to this idea, Sonso infants, who are usually seen interacting with all kinds of vegetation, appear to lose interest in sticks as they grow up.

Some data presented by Biro and colleagues (2003) also support the idea that the key units passed on are not necessarily behaviours. They noticed that, when introducing a new type of nut (coula nut) absent in the core area of the Bossou community, only one adult female, Yo, appeared to know of them and started to crack and eat them. The authors suggested that she had emigrated from a community that consumed these nuts, which was subsequently proven by genetic analysis (Biro et al. 2003; Shimada et al. 2004). The exploration and the consuming of the coula nuts progressively spread in the group, mainly through juveniles that became very interested in these nuts. Interestingly, the introduction of panda nuts, apparently unknown to the whole group, triggered much less interest from the community. Thus, the presence of Yo was the likely factor that influenced the other group members to engage with coula nuts, for which they subsequently applied their knowledge of nut-cracking. However, in this case, it is hard to interpret the observations as the spread of a behaviour because it was already present in the community. Rather, it seems likely that what was transmitted was the idea that this type of nut was edible, which drove other individuals to try to eat them on their own.

In summary, the Biro et al. study and my own experiments suggest that considering chimpanzee culture only at the level of behaviour fails to grasp the entirety of the phenomenon. Exploring chimpanzees at the level of ideas rather than behaviours may bring

an interesting new dimension to existing and new results. Although analysing animal culture as sets of ideas rather than behaviours may be a conceptual challenge, I show in the next sections that this would not change drastically our way of analysing the cognitive processes that are involved in the phenomenon, and could even simplify their study.

**The acquisition of ideas through an attention filter**

Chimpanzees are social animals who throughout their lives are rarely alone at any moment, meaning they are constantly exposed to each other's behaviours (Goodall 1986). In fact, orphans are unlikely to survive if they are too young when they lose their mother, although adoption may happen in rare cases (Boesch et al. 2010). The results I described in chapter 5 suggest that other individuals, especially mothers, may act as an 'attention filter' through which youngsters come to view the world. Chimpanzees spend the first ten years of their life closely associated with their mother and, notably, the first couple of years during which their cognitive mechanisms mature are spent within her immediate contact (Tomonaga 2006). This means that for the two first years of their existence, the only environmental stimuli that they will be confronted with are largely determined by their mother. However, even when gaining in independence, it is unlikely that the influence of the mother and other close associates will fade. Although infants may still pay attention to a wide range of stimuli while discovering their environment, they apparently lose interest in what is not a relevant feature for their parents or older siblings. For instance, adult Sonso chimpanzees rarely engage with sticks, while youngsters, similar to the Kanyawara individuals, often play with them. Sticks therefore become a more irrelevant element of their environment, perhaps because none of their adult models have drawn their attention towards them. A difference in relevance in the environment can have powerful inhibitory effects on learning (cf the 'learned irrelevance' effect, Mackintosh 1974) and this could explain why none of the Sonso individuals developed stick use, even after retrieving the stick from the hole individually. This hypothesis can also be linked to the proposed hypothesis that juveniles want to act like the others surrounding them, defined as the Bonding- and Identification-Based Observational Learning (BIOL) model by de Waal (2001).

Recent observations in the wild support this idea of a filter. Individuals surrounding the youngster build a virtual map of the environment from which certain features are made more salient than others by interesting themselves in certain trees (for feeding or resting), in certain

fruits of a specific degree of ripeness and in plants with medicinal properties (Huffman et al. 2011). As a consequence, the youngster will become more familiar with these particular features. Other features will become less salient, particularly the ones that more experienced group members are not engaging with. This can result in different families and communities consuming different foods because of their 'cultural diet' (e.g. Thornton 2008; Jaeggi et al. 2010a; Muller and Cant 2010). However, the behaviour of the knowledgeable individuals can have further implications, for example by inducing youngsters to develop or lose interest in handling stones (Zuberbühler et al. 1996; Matsuzawa et al. 2001; Wrangham 2006; Leca et al. 2007a).

**The acquisition of ideas in a scaffolded environment**

The focus of most animal learning studies is the way the 'physical behaviour' is acquired rather than the underlying cognitive links (Whiten et al. 2004). For instance, emulation, although originally defined as achieving someone else's goal or 'objectives' (Wood 1989), has mostly been seen as understanding the fact that an object can produce a certain result in the environment, which will cause an attempt to recreate this modification of the environment (e.g. Tennie et al. 2006). The 'framework of ideas' perspective (FI) I propose focuses on the acquisition of ideas, rather than on that of behaviours. Imitation, in terms of understanding why another individual is doing a certain task, does not require more cognitive processes at work than goal-emulation (although it requires also attention to the physical model and precise memories to recreate the physical action that has been seen, which emulation does not). Thus, within the FI, imitation or emulation do not differ, as in both cases, the animal has to understand the idea, before reproducing it by its own means. Additionally, although the FI does not take imitation as the base of culture, as suggested by some researchers (Galef 2009; Tennie et al. 2009; Tomasello 2009), it does not exclude that full-blown imitation is a powerful tool for individuals trying to acquire the ideas of the function of each behaviour.

The second mechanism that has been proposed to be, together with imitation, at the origin of the human cultural mind is teaching (Tomasello 1999). Although some forms of teaching have been found in animals, notably in cooperative breeders (e.g. Thornton and McAuliffe 2006), these forms are not thought to be able to sustain 'human-like' cultural processes (Csibra 2007). As such, teaching has often been seen as the joint mechanism with imitation that could explain human cumulative culture (Tennie et al. 2009). Evidence for teaching in

chimpanzees is indeed nearly absent apart from isolated anecdotal observations (Boesch 1991). Teaching is heavily involved in the transmission of human culture; however, there is no proof that the former is at the origin of the latter (Laland et al. 2009). Additionally, the fact that teaching has evolved in different taxa that do not possess culture (Thornton and Raihani 2010) makes it unlikely that teaching is the only way to acquire culture. While it certainly plays a role in the diffusion of human cultures (see part C), its involvement in cultural transmission should be studied in the context of information transmission.

In order to reconcile the different opposed views on the topic, the philosopher Kim Sterelny has proposed an interesting framework that he has named "hybrid-learning" (Sterelny 2006, 2009). The idea is that naïve individuals always learn within a social environment that is more or less structured by their parents (or more experienced individuals). This notion is closely linked with the notion of niche construction (Odling-Smee et al. 2003) where animals modify their environment by their own actions, which results in novel evolutionary pressures. For instance, beavers constructing a dam will completely change the ecology of their own habitat. Linking this 'scaffolding' to the attentional filter described above, experienced individuals directing their interest to certain kinds of fruit, for instance, will channel non-experienced individuals to adopt the same practices, although they may not be aware that they do. In this respect, 'full-blown' teaching, which includes the awareness of the ignorance of the pupil in the teacher's mind, is the most efficient way of presenting one's environment so that offspring learn the norms, values and behaviours that occur in the said environment (Sterelny 2009). In the FI, where 'hybrid-learning' is likely to play a key role, teaching does not appear fundamentally different from other acquisition mechanisms in kind: the actions of the knowledgeable individuals allow the naïve ones to understand what is important in their environment. However, the results are tremendously different in terms of efficiency, notably through the use of pedagogy (Csibra and Gergely 2006, see part C).

## 2. A cognitive model of culture

### A solution to the social/asocial learning contrast through a disjoint acquisition model

Although researchers are still debating which learning mechanisms are responsible for the emergence of the different patterns of behaviour observed in animals (Galef 2009; Tomasello 2009; Whiten 2009), it appears likely that a range of learning mechanisms occur in chimpanzees, as much as they do in children (Horner and Whiten 2005; Whiten et al. 2009). The main cause of the overdeveloped interest for imitation was the claim that imitation was the support mechanism for culture, and especially cumulative culture (Tomasello 1990; Galef 1992; Tennie et al. 2009). However, recent experiments with humans have shown that simple behaviours can be transmitted through populations without the need to resort to imitation (Caldwell and Millen 2009), which raises doubts about the real impact of imitation in the propagation of culture in humans, especially during the early phases of human speciation. Second, although it is important to precisely determine what is happening during animal learning, the question of culture will not be solved by solving the problem of imitation as social learning is not equivalent to culture (McGrew 2009). As far as animal culture is the main topic of discussion, a definition of imitation like the one proposed by Thorndike in the late XIX $^{th}$ century: "learning to do an act from seeing it done" (1898) may well encompass the most important criterion of social learning when dealing with culture: observation.

The current consensus is that a number of mechanisms, including imitation, are at play during animal learning (Laland and Galef 2009b) and developmental results obtained in the wild suggest that learning is a mix of social influences and individual trial-and-error learning (Matsuzawa et al. 2001). As a consequence, individual and social learning should be studied together as they probably coevolved together, the abilities being used during social learning enhancing an animal's individual learning abilities (van Schaik and Burkart 2011). Social learning was originally defined as the contraction of "socially-biased learning" or even "socially-biased individual learning" (Galef 1995; Fragaszy and Visalberghi 2001), which finds echoes in the hybrid-learning or FI perspective. However, while these researchers put the emphasis on the 'individual learning' part of the definition, the FI suggests on the contrary that the important part is the 'socially-biased' one. In a way, it does not matter up to which point an animal is influenced by others, as long as it acquires the idea from them. This

influence can consist of indicating that something may be done there (local enhancement) up to how to handle a stone (production imitation).

My proposal to adopt a novel framework appears here useful: it does not matter which social mechanism is at work during the development of the behaviour, as long as there is at least a definitive social influence in the acquisition of the *idea*. In effect, the FI perspective proposes to study how an individual acquired the idea of performing a certain behaviour, rather than the behaviour itself. This shift allows one to deconstruct the acquisition of behaviours in two steps: acquiring the idea from observing others, then developing the behaviour individually, most likely through trial-and-error processes, with a possible feedback from more experienced individuals (through teaching in humans, see below). The distinction proposed by Byrne between production imitation and programme-level imitation is especially applicable to this framework (Byrne 1994; Byrne and Russon 1998). Young gorillas, rather than copying each step without knowing where to go, appear to acquire the general plan of how to process nettles, but have to work out the details on their own during their development. Similarly, young chimpanzees in Bossou are thought to master nut-cracking through a master-apprenticeship relationship, where observation of the behaviour of skilled masters and individual and unrewarded trial-and-error learning are two necessary components to learn fully how to crack nuts (Inoue-Nakamura and Matsuzawa 1997; Matsuzawa et al. 2001; Biro et al. 2003). Here again, young chimpanzees need to acquire several ideas during their development. First, they have to understand that nuts contain edible food, which is done mainly through scrounging (which could happen without social influence if a nut happened to be open, although chimpanzee food conservatism, again, would probably prevent a chimpanzee from exploring this food on his own, unless forced). Second, they need to understand that to obtain this food they have to break the nut open, through the use of a stone. This fundamental idea that a stone can be used as a tool appears unlikely to be discovered by chimpanzees on their own, given the apparent limitations that wild chimpanzees experience when confronted with the end result only. Although 10 of 20 Sonso chimpanzees retrieved the leafy-stick from the honey trap, experiencing directly the fact of using it as a tool, they did not make this conceptual connection in their brain, something that I explained by the fact that they had never witnessed others using sticks as tools (see chapter 5).

**New innovations based on current knowledge: A case point for cumulative learning**

While the word 'culture' is again in use to qualify the community-specific patterns of behaviours found in diverse animals, these cultures are thought to be very limited and to lack most of the cumulative characteristics of human cultures (Tomasello 1999; Tennie et al. 2009). Recent experiments in sanctuaries have shown that chimpanzees, after learning a technique that generates a reward, do not upgrade to a technique similarly demonstrated and which brings more reward than the first one, a phenomenon named 'conservatism' (Marshall-Pescini and Whiten 2008; Hrubesch et al. 2009). For the authors of the first study, this finding may "[constrain] the species' capacity for cumulative cultural evolution" (abstract). However, another interpretation may be possible. Chimpanzees may be satisfied with the quantity of reward they obtain with the first technique, and become 'stuck', not because they cannot build on their initial knowledge, but because they are less likely to pay attention to or remember a new technique, if they already have in mind a technique that will anyway grant them some reward. Additionally, results found in sanctuary-raised animals are unlikely to apply to wild individuals, as far as they concern ecological pressures such as developing a novel feeding technique to survive. These individuals are fed daily and know that the accumulation of test trials will bring an accumulation of rewards for themselves. Therefore, there is no urgent need for them to learn these new techniques.

Data from the wild, however, may indicate another way of thinking about cumulative culture, notably in the early phases of human speciation. Recently, Yamamoto and colleagues (2008) described how a juvenile individual, JJ, adapted the customary ant-dipping of its Bossou community, which normally only occurs on terrestrial ants (Humle and Matsuzawa 2002), to arboreal ants. Within two years, the tools he used to fish for these ants became significantly shorter than the ones used to dip for terrestrial driver ants, a modification which suited the characteristics of arboreal carpenter ants (Yamamoto et al. 2008). The authors proposed thus that the behaviour, which was originally intended for the fishing of ants on the ground, may have been adapted to the fishing of arboreal ants to match their characteristics. Such an observation supports an idea of cumulative culture different from what has been proposed. Tomasello and colleagues argue that cumulative culture encompasses solely behaviours that could not possibly be developed within one generation (Tomasello 1999; Tennie et al. 2009). However, the observations of Yamamoto and colleagues (2008) suggest that cumulative culture could be seen as building on one's knowledge to develop new behaviours, not necessarily with any time span having to be taken into account. This question of time span is

also apparent in the cultural debate in general, and some authors have suggested that transmission through generations may not be a critical condition for a behaviour to be a tradition (Fragaszy and Perry 2003b, p. 24-25). Similarly, human fashions (for instance, the games that every one of us played at school), which are definitely cumulative as they build on centuries of technology, do not necessarily last more than a generation.

Thus, in order to identify cumulative culture, the focus should be on the cumulative characteristic itself, which consists in building on or adapting existing knowledge (Gibson 1993; Parker and McKinney 1999). My results with the Sonso community support this notion. Individuals at Sonso responded to the honey-trap test by adapting an existing behaviour, leaf-sponging, to the problem. Leaf-sponging has never been observed in the wild as a means to collect honey, although leaves are occasionally consumed together with honeycombs. However, a sponge is not a practical tool to consume waxy honey. It is only because the provided honey was liquid that the sponge became a potentially good solution. In other words, the chimpanzees who adapted leaf-sponging to the consumption of honey probably noticed that the liquid consistency of the honey was similar to that of water and that leaf-sponging could be used to extract it. Similarly, JJ built on his previous knowledge to adapt a behaviour used originally with ants to fish for another species of ants, modifying the tool in the process.

Byrne (2002) introduced the notions of contextual imitation and production imitation, based on the notions of contextual and production learning proposed by Janik and Slater (2000). Where production imitation allows the learning of a new behaviour that was not previously in the repertoire, contextual imitation allows one individual, after seeing a conspecific using a behaviour that is part of their common repertoire in another context, to copy the old behaviour in the new context. These two definitions have to be connected with the numerous discussions on animal innovation (for a review, see Reader and Laland 2003). Similarly to animal culture, animal innovation is defined behaviourally and most of it consists of modifying existing behaviours to new contexts (Kummer and Goodall 1985; Reader and Laland 2001). Definitions of human innovation, in contrast, are based on ideas (e.g. Rogers 1995). Within the FI, innovation can be seen the use of an idea already known by an individual to solve a novel problem, or to solve an ancient problem with a novel technique. Here again, the principal motor is the underlying idea, rather than the surface behaviour. The animal must have a certain idea of the problem and how to solve it. In Yamamoto et al. and my studies, individuals did not come blindly to the problem, they had already learnt their

community-specific tool use repertoire, and they adapted a skill they had already fully mastered to a new problem. The development of Wheat Placer Mining (WPM) in Koshima (Kawai 1965; Watanabe 1994; Hirata et al. 2001) can also be analysed from this perspective: Imo, who first developed SPW, adapted this knowledge to the washing of a new substrate, wheat. The idea of washing food may be here also more important than the behaviour itself.

A final point that deserves more research in the future is that in both chimpanzee studies and macaque studies, the individuals who adapted a behaviour to the new situation were mostly juveniles or young adults (Zuberbühler et al. 1996; Hirata et al. 2001; Yamamoto et al. 2008, see chapters 4 and 5). In contrast, the behaviour hardly developed in older individuals. This observation, if confirmed, has a consequence in terms of the underlying mechanism: it is unlikely that the capability for innovation relies only on response facilitation (Byrne 1994). If such were the case, adults, who have developed strong neural connections through the repeated performance of a behaviour, should be faster than juveniles with limited experience to adapt this skill to the new task, and we observe the opposite situation. On the contrary, it is likely that innovation is mostly developed by juveniles because adults are entrenched in a routine that may prevent them from experiencing new techniques. In my studies, a number of mothers saw their offspring manufacture leaf-sponges and obtain honey out of it. However, only one manufactured a leaf-sponge during the same bout as her offspring and no other adult manufactured a tool to access honey in Sonso. Therefore, the plasticity of the brain in young individuals is probably what allows them to adapt behaviours to novel contexts. On the contrary, the maturation of the brain may prevent adult individuals from learning new techniques. We can relate this to the relative difficulty of older generations in adapting to new technologies in humans (e.g. Charness and Boot 2009).

**Intelligence, culture and cognition**

Several models have attempted to explain the origin of primate intelligence. Some attribute the origin of primate intelligence to certain pressures, whether social (Byrne and Whiten 1988; Dunbar 1998, 2003) or physical (Parker and Gibson 1979; Byrne 1997). Some recent models, however, attempt to analyse non-human primate intelligence under the framework of general intelligence (Reader et al. 2011; van Schaik and Burkart 2011), building on current views of human intelligence, which is seen as a broad domain of general competence (Gottfredson 1997). In this respect, intelligence appears to have an old evolutionary history

(Byrne 1995). These models also attempt to link general intelligence with culture in animals (Reader et al. 2011; van Schaik and Burkart 2011), in contrast to other models which separate the human cultural mind as an exception within the primate realm (Tomasello 1999; Herrmann et al. 2007). In these models, behavioural flexibility is a key point as it sustains the capacity for innovation (Reader and Laland 2003), and a useful approach to compare species' general intelligence is to compare their propensity to engage in behavioural flexibility (Reader et al. 2011). With respect to culture, the authors found that propensities for tool use, social learning and behavioural flexibility were positively correlated, suggesting that culture should not be taken apart from models of intelligence in non-human primates, but rather, included as a part of a general intelligence which evolved several times independently in different species (Reader et al. 2011). Van Schaik and Burkart's model also assumes that, within a general model of intelligence, animals that benefit from social learning will also be more efficient in their individual learning processes, as the modules in use during social learning such as attention or memory are also in use during trial-and-error learning processes (van Schaik and Burkart 2011). Comparisons of 'abnormal' animals, either socially deprived (Mason et al. 1968; Menzel et al. 1970) or 'enculturated' (Hayes and Hayes 1951, 1952), suggest that in conditions which favour an important social exchange, chimpanzees develop faster and stronger abilities, notably in terms of tool use and technical skills (Bard and Gardner 1996; Call and Tomasello 1996; Tomasello and Call 2004).

Another relevant point is what animals are exposed to during their ontogeny. While genetics, through both the species-specific genome and the individual-specific parental inheritance, code for general capacities, the continuous feedback during ontogeny between the set of learned skills and the skill pool of the population is responsible for the development of an individual's cultural repertoire. When animals have learnt a certain tool behaviour, they will use it when needed, allowing their offspring to get a reliable model to acquire the idea from. However, if ecological changes bring more easily accessible food within reach, the behaviour is not going to be reproduced and the offspring will lose their model. Theoretically, one generation is enough to completely lose a behaviour, if it is not being demonstrated by the older generation to the new generation. However, what is lost is not the capacity for the behaviour, only the idea. If a behaviour can be lost, it can also reappear easily, as long as a model and time to experiment are available to build on the ideas being transmitted. Chimpanzees in captivity, even of the *P. t. schweinfurthii* subspecies, which has not been observed nut-cracking in the wild, easily learn nut-cracking from their human keepers

(Marshall-Pescini and Whiten 2008). Cultural acquisition should thus be seen as the application of the general ability to think and have the time to do so. Wild adult animals that need to acquire their daily amount of food will not possibly find the time to design a new way of solving problems if their normal routine can already bring the necessary calories for the day. However, young individuals who are more plastic and can also rely on their elders to obtain a food source, may apply the techniques they know to a new substrate and develop new techniques by these means. Linking environmental variations and persistence of behaviours in a population may also suggest that the development of new feeding behaviours may only be triggered by abnormal conditions that push an individual to explore new options, leaving space for individual innovation and intelligence (Hauser 1988; Lee 1991, 2003).

## 3. Ideas in the cultural debate: Definition, operationalisation and use

The preceding paragraphs as well as recently published studies have shown that there is probably more to chimpanzee cultures than differences in behaviours between communities (Whiten et al. 2003). I have adopted the view that culture could be assessed as a conglomerate of ideas, or '*mental representations*', rather than a conglomerate of behaviours. Different communities of chimpanzee may have different knowledge composed of different sets of mental representations. In other words, what is important in honey-fishing is to know that to obtain honey, one must use a stick, so that the activity of 'using a stick as a tool' is connected to the activity of 'obtaining honey'. The knowledge of 'honey-fishing' is therefore a set of several pieces of knowledge connected together in one's mind.

The problem that we face is that we need to analyse differences at the cognitive level that are only observable at the behavioural level. However, the experiment described in chapter 5 is especially valuable in this respect as it highlights that differences in knowledge lead individuals to find different parts of the same tool salient. The concept of 'salience' is therefore central to the operationalisation of 'cultural ideas'. While the environmental stimulus is the same for the two communities, the behavioural difference found can only result from deeper cognitive causes. Each subject individually used the provided tool in the way it found it the most appropriate. Within groups, individuals were clustered by

community knowledge, linking cultural knowledge and cognition. I thus propose to study ideas through the filter of salience.

My proposal to rely on salience to study ideas can be seen as highlighting two elements in the animal culture debate. Firstly, it points out the importance of cognition. Similarly to what is observed in the human literature (e.g. Haun and Rapold 2009), cultural differences at the cognitive level can be reflected at the behavioural level. These paradigms may thus help to decipher the links between culture and cognition. Secondly, focusing on salience also brings another way of addressing the problem of social learning. The experiments described in chapter 4 and 5 show that chimpanzees of a given community fail to grasp what is salient for the other community. Therefore, it is likely that this salience (as argued above) is acquired through social learning. Studying how certain features of one's environment become salient for a naïve individual therefore is a way of understanding how social learning builds cultural knowledge. As such, if salience can be unequivocally connected to a social input, it may thus resolve one of the main current debates in the animal culture discussions.

## C. Perspectives and conclusions

### 1. Perspectives: Chimpanzee culture and human cultural uniqueness

In parts A and B, I have tried to reconcile the main opposing views in the animal culture debate. In part A, I have proposed that, instead of attempting to isolate the major influence that triggers the development of a behaviour and its geographic variation between different communities (which will bring inevitably future questions of the 'how much variation has to be attributed to culture to make a behaviour cultural?'-type), a model assuming an impact of all factors in the development of these differences is the less controversial and the most likely to reflect reality, given the complexity of the phenomenon studied. Given the accumulation of data both from studies in the wild and in captivity, it is now accepted that chimpanzees acquire some of their behaviours through social learning (Whiten et al. 2009) and that some of these behaviours qualify as cultural. Hence, if culture is defined in behavioural terms, there is little doubt that chimpanzees have culture.

Most researchers working on culture in humans, however, would not agree that chimpanzee behaviours should be considered as cultural, largely because their definitions are based on mentalistic notions. Therefore, in part B, I have discussed some of the results presented in my empirical chapters in this light and proposed a more cognitive model of animal culture. I then explored whether animals' minds could be studied and assessed fruitfully for cultural components, as it has been done for human minds. I concluded that this is the case of chimpanzees. In this species, culture appears to be deeply entrenched in their minds, similar to what is found in humans, which may narrow the gap between the two species even more. Therefore, even if a 'human approach' is adopted to study chimpanzee cultures, it seems that chimpanzees could still be granted a certain cognitive culture.

However, after reaching this point, it must be nonetheless underlined that even the most 'primitive' hunter-gatherer cultures still are far more complex than any non-human animal culture. While I have already discussed some theories of human culture in the preceding parts, notably linked to imitation and teaching, I have shown that the arguments they proposed did not appear consistent with recent captive and field data obtained notably with chimpanzees. Nonetheless, as humans, we do not simply have community-specific sets of ideas; we value them and are ready to fight for them. We also attach a meaning to certain practices. Although a number of social traditions are observed in the wild in several species, for instance in cetaceans (Rendell and Whitehead 2001) or capuchins (Perry et al. 2003a), and may act as social markers, it is noteworthy that all human groups without exception attach a strong identity marker to some of their practices (for instance, see introduction in Henrich et al. 2010) and it is far from clear that other animals do the same. From the form that was present in the chimpanzee and human ancestor, different aspects of cultures differentiated in the human lineage, probably in relation to cognitive changes that appear to be most developed in humans: the emergence of a full-blown theory of mind and of an articulate language (Tomasello 1999). These cognitive developments may have allowed humans to reflect about their own knowledge, not simply in order to transmit it to their offspring, but also to realise that this knowledge constituted 'a way of doing things' in their group, which became operationalised by the implementation of norms as well as the will to conform to them (Whiten et al. 2005).

## 2. Perspectives: Limitations of the current work and solutions

In this discussion, I have shown that adopting a framework of ideas changes much of our understanding of animal cultures. However, there are still questions that remain unanswered and here I briefly summarise the limitations of my work and what could be done in future research to complement the studies I have presented in this thesis.

### Are tool-using behaviours acquired through social learning?

In chapters 4 and 5, I have shown that field experiments are a useful tool to test cultural differences between communities. However, as in Biro and colleagues' (2003) study, the evidence is only indirect. My conclusion that the presumed cultural variant 'fluid-dip' is indeed cultural is based on the segregation of the behaviours between the Sonso and Kanyawara communities, and thus, supported only by statistical analysis (Laland et al. 2009). Although this segregation was absolute, suggesting that stick use and sponge use (which is also a chimpanzee universal) were used in a cultural way, this does not bring conclusive evidence that the behaviours have been learnt through social learning. Rather, the tests I have presented can be seen as a way of testing that a certain behaviour, here, 'fluid-dip', is really absent in the Sonso community, and that individuals are unlikely to develop it on their own without any demonstration. Critics may thus argue that this method, although more rigorous, does not bring much more than the initial 'exclusion method' in showing the cultural characteristic of the behaviour. What remains to be done is to implement an experiment that seeds a novel behaviour in a community and study its transmission. The data presented in chapters 4 and 5 can constitute support for the claim that stick use does not develop through individual trial-and-error learning in chimpanzees. The Sonso community has been exposed extensively to a range of conditions that could have triggered stick use but did not, showing that some key factor was missing. The direct demonstration of the behaviour to the chimpanzees is the only condition I did not test in Sonso, as the main goal of the studies presented here was to see how wild chimpanzees used their knowledge to engage with their environment without human interference. A human demonstration would thus have not been a natural setting to study the emergence of tool use in wild chimpanzees. However, such a demonstration may be the only way to seed this behaviour in the

community and future studies should address this condition to find out if it would trigger an individual to develop the behaviour. Such a study could bring the definitive proof that observational learning is necessary in the transmission of tool use in chimpanzees, if the behaviour is transmitted subsequently in the group.

**How to explain these results in light of chimpanzee innovation?**

The most surprising result presented in this thesis is the refusal of Sonso chimpanzees to adopt the stick use behaviour. Although it makes sense that individuals who adapted leaf-sponging to solve the task did not pick up on this behaviour, it is less understandable for individuals who remained unsuccessful in this task. These results can be interpreted in two ways. First, they are the ground for the theory that I have developed about chimpanzees' cultural mind. This is the first experiment that shows that chimpanzees' learning abilities seem to be constrained by their knowledge. Results from chapters 4 and 5 show that two different chimpanzee communities can approach the same problem differently, independently of the affordances of the task, and that they appear to experience a cultural bias, related to the cultural override found in humans (Haun et al. 2006b).

However, the second effect of these results is that they raise numerous questions about wild chimpanzees' abilities to innovate. In chapter 1, I have reviewed a body of data showing that chimpanzees' physical cognition is well developed, and in many ways equivalent to human infants' (Herrmann et al. 2007). Similarly, observations of complex tool use in the wild are accumulating (Matsuzawa 1991; Sanz and Morgan 2007). Finally, chimpanzees are amongst the top species in terms of the ability to innovate, according to Reader and Laland's analyses (Reader and Laland 2002). My results show, in contrast to these results, that it seems hard for chimpanzees to invent or re-invent even 'easy' behaviours, such as fluid-dip, especially in comparison to the multiple steps required for nut-cracking. This observation can theoretically support the social learning hypothesis: if a behaviour does not develop even when individuals are given the opportunity to perform it by themselves, it is unlikely that it emerges frequently in the wild, suggesting that its spread is the result of a social transmission. Nevertheless, the behaviour must have been invented by someone in the first place and my results are not informative concerning this question, apart from the idea that 'genius' individuals, such as Imo, may be needed. Alternatively, it is possible that innovation is driven by necessity. For instance, harsh conditions may trigger the development of novel

feeding behaviours that remain parts of a group behavioural repertoire. Future studies will need to address chimpanzee innovation both experimentally and through observations (Nishida et al. 2009) to understand which conditions are necessary for it to occur in the wild.

**Are these results applicable to other chimpanzees and other species?**

Another matter is the relevance of these data to other chimpanzee communities and other species. Ugandan chimpanzees in general appear to be more limited in their tool-using abilities compared to chimpanzees of other areas (McGrew 2010). Thus, the results found with the Sonso chimpanzees may be specific to their origin and location. Although this is unlikely, given the high genetic relatedness of Eastern chimpanzee populations (Goldberg and Ruvolo 1997a), more experimental data have to be collected from other chimpanzee populations. I have already shown in chapter 6 that what is found in Sonso is likely to be the norm within the Budongo forest, although more results are needed to strongly support this assumption. More generally, it would be interesting to study if the cultural bias found with Ugandan chimpanzees is found in other chimpanzee subspecies, notably in communities that have a larger catalogue of tool-using behaviours. Several questions arise. First, it would be interesting to document the existence of a culturally-biased selection in other behaviours than 'fluid-dip' and 'leaf-sponge'. Second, new theoretical models of intelligence suggest that cultural knowledge and individual cognitive abilities are linked (Reader et al. 2011; van Schaik and Burkart 2011). Implementing field experiments in chimpanzee communities that have a more developed cultural knowledge than the Ugandan chimpanzees may therefore bring new insights in how chimpanzee cognition and culture are linked.

A related question is how adaptable such studies are to other species than chimpanzees. The protocol that I developed originally aimed at testing particular behaviours that are presumed to be cultural. Therefore, in theory, there is no limit to the species to which the paradigm could be adapted, as far as a suitable behaviour is found. The results these studies could bring are of tremendous importance. If the cultural bias were found in species other than chimpanzees, this would mean that the 'cultural mind' evolved much earlier than expected. In other words, animal cognition may have been influenced by their cultural knowledge in how they comprehend their environment for a long time. However, the results could also come with certain species having community-specific patterns of behaviours but reacting in species-specific ways to the tools, independent of the community of origin. If such were the

case, then the most parsimonious explanation would be that the animals are reacting to a particular affordance of the tool, independent of their community knowledge. As a consequence, the species' 'culture' would not be considered in the same way as human or chimpanzee cultures. With an increasing number of species and behaviours tested, such a method would allow us to draw a line between species that can be characterised with a cultural mind, such as humans and chimpanzees, and other species, that display an analogous cultural distribution of behaviours, but which only results from environmental affordances.

**Are chimpanzees aware that they have cultural ideas?**

Throughout this thesis, I have defended the position that we cannot understand what makes us truly humans if we do not understand what is common between us and chimpanzees. I have argued that the most commonly given explanations, imitation and teaching, are unsatisfactory, given experimental evidence found in captivity (Whiten 2009). Based on my results, I have proposed that culture in chimpanzees is deeply entrenched in their mind. However, my results cannot show that they are aware of their own culture, in the same way as we humans are. To be able to do so, they would need to display some aspects of self-reflexivity, or the use of "an integrated representation of one's own mental, social and physical dispositions" (*sensu* Proust 2003), which is central in how humans comprehend themselves in the physical world. My results suggest that chimpanzees may be unable to go mentally through their tool-using catalogue, and select an option that could best suit the task to solve a problem. Most likely, they are using what they already know, and can hardly overcome the ontogenetic influences that were applied to them, unconsciously, by their mother. However, contradictory results obtained in Sonso between adults and juveniles raise further questions. One explanation is that the youngsters only tested a behaviour that they knew and found that it was working on such a task, while adults did not have the plasticity to do so. However, the youngsters may have selected the behaviour knowing the requirements of the task, therefore showing a certain representation of their own knowledge. My experiments are inconclusive in this respect, and more generally, experiments in the wild are unlikely to propose the correct format to test this hypothesis. Rather, more controlled experiments in captive settings may be necessary to understand how chimpanzees deal mentally with their own knowledge, as it requires knowing exactly what an individual is exposed to during its ontogeny and during the demonstration of a new task.

## 3. General conclusion

As Darwin suggested in 1871, human and animal minds do not differ fundamentally in kind (Darwin 1871), and the data presented in this thesis suggest that this remark holds for their cultural mind as well, at least for chimpanzees. Over the last 50 years, research in the field and in captivity has generated plenty of evidence to support this idea. Some critics will still argue that ecological reasons can be invoked to explain community-specific patterns of behaviours, based on the assumption that we will never be able to identify all possible ecological factors that may be responsible for these differences. Yet, I have shown that no factor should be dismissed in the building of behaviours, and that genetics, ecology and social mechanisms are all necessary for the emergence and maintenance of cultural behaviours. However, I have also argued that considering chimpanzee cultures as conglomerates of behaviours limited the number of evolutionary questions that could be asked and probably missed a great part of the phenomenon. My results show that there is a deep cognitive side to chimpanzee culture that is yet to be explored. They suggest that chimpanzee cultures are conglomerates of socially acquired ideas that filter what a youngster is exposed to during ontogeny. The role of a model may thus be central to the establishment of these cultures, although there may well be no cognitive motivation of the model to perform as one in chimpanzees, while in humans, the model is fully conscious of the impact it has on its offspring and can orient its attention to certain features of the environment. Related to this, a central point of this thesis is that, although we need to reconsider chimpanzee cultures closer to the phenomenon described in humans (making them good models of what early hominid cultures were like), there is still an important gap between chimpanzee and human cultures. Human cultures are unique because a number of cognitive processes have coevolved together in our own lineage. A very important step in our cultural evolution was to become aware of our own knowledge, and to realise that this knowledge was not necessarily shared by everyone, within or out of the group, and it remains unclear if chimpanzees have this kind of knowledge. A Kanyawara chimpanzee may well not mind seeing a Sonso chimpanzee using a sponge to acquire honey, because he is not aware that he is doing otherwise in his own culture. Similarly to Monsieur Jourdain in Moliere's play, chimpanzees appear to practice their art without knowing that they do. Only research will tell if this may be what separates our cultural mind from its primate roots.

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# Appendices

**Appendix A.** The remote video camera at the location of the first set of experiments in Sonso, Budongo Forest. The Raphia tree is in the foreground (picture by T. Gruber).

**Appendix B.** Beck (1980)'s classification of tool-using behaviours per context with associated pages in Beck, B. B. 1980. Animal tool use. New York: Garland Press.

| Context | # | Page | Action | Behaviour | Description |
|---|---|---|---|---|---|
| Antagonism | 1 | 79 | Brandish tools | Agonistic intimidation displays | Wild: Chimpanzees brandish or wave uprooted tools at others, human observers, animals (live or model), own mirror images. Captivity: at conspecifics, humans, animals (live or model) |
| | | | | Immature Agonistic intimidation displays | Once brandished twigs towards a young female in a miniaturised version of adult male display |
| | | | | Sticks in rain storm | Brandish sticks during explosive episode of excitement and animated locomotion triggered by a rainstorm |
| | | | | Wave tools against flies | Wave boughts to disperse swarming flies |
| | | | | Sticks in play | Brandish sticks during play |
| | 2 | 80 | Dragging tools | Dragging, rolling, and/or kicking objects during display | Conspecific Dragging, rolling, and/or kicking objects during display in the presence of conspecifics |
| | | | | Dragging, rolling, and/or kicking objects during display | Heterospecific Dragging, rolling, and/or kicking objects during display in the presence of baboons |
| | | | | Drag branches during rainstorm | Expression of general excitment rather than of social agonism |
| | | | | Dragging during social play | Dragging |
| | 3 | 81 | Unaimed throwing | Unaimed throwing in arousal states | Throw without aiming during intraspecific agonistic charging displays and rain dances, or when frustrated by unsuccessful attemps to gain access to incentives such as estrous females |
| | | | | Unaimed throwing in reaction to stimuli | Throw without aiming during model or playback experiments or in the presence of other species (baboons, goat, mangoose). Captivity: in the presence of hippopotamus |
| | | | | Unaimed throwing during social interaction | Throw without aiming during agonistic charging displays in the presence of conspecifics and humans |
| | | | | Unaimed throwing resulted from frustration | Throw without aiming when frustrated from unsuccessful attempt to reach food |
| | | | | Unaimed throwing during play | A variety of objects are thrown without aiming during play |
| | 4 | 82 | Aimed throwing | Aimed throwing during agonistic interaction | During fights, aim and throw tools at conspecifics |
| | | | | Interspecific aimed throwing | Wild: Throwing objects at other species. Captivity: Throwing sticks at other species such as humans, a tiger and dogs; and at fear-producing stimuli such as reptile models |
| | | | | Interspecific aimed throwing (hunting) | Throwing sticks at other species during predation |
| | | | | Aimed throwing during social play | Aimed throwing during social play |
| | 5 | 83 | Dropping | Interspecific dropping | Wild: Drop branch when descent from trees is blocked by humans or in presence of a leopard model. Captivity: Drop tool on human |
| | | | | Conspecific dropping during social play | Drop branch on conspecifics during social play |
| | 6 | 84 | Clubbing | Conspecific clubbing | Club or hit conspecifics during agonistic episodes |
| | | | | Interspecific clubbing | Club or hit another species |
| | | | | Social play conspecific clubbing | Club each other during play |

| Context | # | Page | Action | Behaviour | Description |
|---|---|---|---|---|---|
| Antagonism (continued) | 7 | 85 | Prodding or jabbing | Conspecific prodding or jabbing during agonistic contexts | Prodding or jabbing during agonistic contexts |
| | | | | Interspecific probbing or jabbing | Prodding or jabbing other species during agonistic contexts |
| | | | | Insect spearing | Spear insects with lengths of straw |
| | 8 | 100 | Tree pounding | Pound on tree buttresses during agonistic displays | Pound on tree buttresses (or other noisy object) during agonistic displays |
| | 9 | 100 | Frustration pounding | Pound on objects after unsucessive attempts | Pound on objects after unsucessive attempts |
| Grooming | 1 | 91 | Dental grooming | Dental Allogrooming | Scrape at or probe in the other's teeth |
| | | | | Dental Autogrooming | Scrape at or probe in one's teeth |
| | 2 | 91 | Grooming | Interspecific Grooming | Probe in different body parts of another species |
| | | | | Self-Grooming using tools | Self-Grooming using tools |
| Escape | 1 | 91 | Escape enclosure | Use of sticks as pitons to escape enclosure | Use of sticks as pitons to escape enclosure |
| Play | 1 | 91 | Infant Termite fishing | Insert and Probe in mounds or nests of termites | Insert and Probe in mounds or nests of termites |
| | 2 | 100 | Playful pounding | Pound objects on others for playful purpose | Pound objects on others for playful purpose |
| | 3 | 101 | Playful exploration | Exploration with stick | Pry in crevices |
| Oddness/ Inaccessibility | 1 | 94 | Using tools when reluctant to touch with hand | Touching inhabitual objects | Use of sticks to probe inhabitual, fear-producing and potentially dangerous objects |
| | | | | Interspecific Touching | Use of sticks to probe another species |
| Balancing and climbing | 1 | 95 | Secure object | Secure object (e.g.: suspended food) | Use of stick to secure food |
| | 2 | 95 | Playful balancing | Playful balancing | Use of pole for playful purpose |
| Propping and climbing | 1 | 96 | Secure suspended food | Secure suspended food | Use of stick to secure food with the topmost tip of the stick or pole placed against a vertical surface |
| | 2 | 97 | Escape enclosure propping | Escape enclosure propping | Use of tool as ladder with the topmost tip of the stick or pole placed against a vertical surface to escape the enclosure |
| Stacking | 1 | 97 | Access to suspended lures or to extended vision | Gain access to suspended lures or to extended vision | Stack objects and climb them so as to reach inaccessible goals |
| | 2 | 98 | Escape enclosure stacking | Escape enclosure stacking | Stacking objects to be able to escape |
| Food acquisition | 1 | 85 | Termite fishing | Insert and Probe in mounds or nests of termites | Insert and Probe in mounds or nests of termites |
| | | | | Perforate termite mound | Use stick to perforate termite mounds |

| Context | # | Page | Action | Behaviour | Description |
|---|---|---|---|---|---|
| Food acquisition (continued) | 2 | 87 | Ant Dipping | Dipping for fossorial ants | Pull and scrape out handfuls of soil which stimulates massed active aggression by the soldiers. The ape then selects and/or modifies a branch and inserts it into the nest |
| | | | | Dipping for arboreal ants | Insert tool in the nest holes in trunks and branches |
| | 3 | 89 | Wild: Honey fishing. Captivity: Artificial fishing | Insert tool and probe in bee/artificial nest | Insert tool and probe in bee/artficial nest |
| | 4 | 93 | Reaching food or object | Reaching and retrieving food lures or objects | Using tools or a series of tools to reach and retrieve food or object |
| | 5 | 98 | Opening tough rinds or shells | Nut cracking | Using a rock to smash open nuts on rocks or trees |
| | | | | Hard-shell fruit cracking | Using a rock to smash open hard-shell fruits on rock or trees |
| | 6 | 100 | Leverage or enlargment of openings | Nest opening | Use stick to open or separate nest from branches or enlarge openings or open sturdy boxes containing bananas |
| | 7 | 102 | Ant wiping | Ant wiping | Use a clump of leafy boughs to wipe ants |
| Digging | 1 | 101 | Digging | Digging | Digging |
| Cleaning | 1 | 102 | Cleaning body | Cleaning body, wound or menses | Cleaning body to wipe blood, feces, urine, ejaculate, sticky food residues and juices, water, mud |
| | 2 | 103 | Cleaning cages | Cleaning outer space | Cleaning cages |
| Liquids | 1 | 90, 103 | Water sucking | Insert tool into concavities | Insert tool into concavities containing water or plain water and suck from it |
| | 2 | 103 | Leaf-sponging | Leaf-sponging | Insert masses of leaves and use them as sponges to absorb the water |
| | 3 | 103 | Fluids absorbing | Fluids absorbing | Sponges to absorb residual fluids and brain tissue from the skull of victims, or fruits |
| | 4 | 103 | Containers | Fluid container | Using any kind of tool as a recipient |
| Baiting | 1 | 104 | Baiting | Baiting | Using any kind of object to bait animals to lure them within reach |
| Draping | 1 | 104 | Draping | Draping | Draping objects on one's body |

**Appendix C.** List of bonobos in group 1 at Lola ya Bonobo at the time of chapter 3 study.

| Name | Code | Age (y) | Offspring |
|---|---|---|---|
| Females | | | |
| Mimi | MM | 26 | x |
| Opala | OP | 13 | Pole |
| Semendwa | SW | 12 | Elikia |
| Bandundu | BD | 11 | Wongolo |
| Kalina | KL | 11 | Malaika |
| Isiro | IS | 11 | x |
| Salonga | SL | 11 | x |
| Nioki | NO | 10 | x |
| Lukaya | LK | 8 | x |
| | | | |
| Males | | | |
| Manono | MN | 14 | |
| Tatango | TT | 14 | |
| Kikwit | KW | 11 | |
| Beni | BN | 10 | |
| Mixa | MX | 10 | |
| Ilebo | IB | 7 | |
| Kindu | KD | 7 | |
| Matadi | MA | 7 | |
| Kasongo | KG | 6 | |

**Appendix D.** Natural bee nest of African honey bee (*Apis mellifera*) on the trunk of a *Premuna angolensus*, Kibale National Park, Uganda (picture by T. Gruber).

**Appendix E.** Settings proposed to the Sonso chimpanzees to enhance the examination of the 'leafy stick' (pictures taken at Sonso by T. Gruber).

(a): bare part inside the hole, free of the combs, in contact with honey;

(b): bare part through the comb and inside the hole, in contact with honey;

(c): leafy part inside the hole, in contact with honey;

(e): leafless, chewed 40 cm stick;

As a comparison, initial setting (obligatory condition, no stick next to the hole, (f)) and stick next to the hole setting (g) are also presented.

(d): bare part inside a 3x3 cm hole is not represented.

(a): bare part inside the hole, free of the combs, in contact with honey

(b): bare part through the comb and inside the hole, in contact with honey

(c): leafy part inside the hole, in contact with honey

(e): leafless, chewed 40 cm stick

(f): obligatory condition, no stick next to the hole

(g): stick next to the hole